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The maxillo-labial complex of *Sparasion* (Hymenoptera, Platygastroidea)

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Abstract

Hymenopterans have evolved a rich array of morphological diversity within the maxillo-labial complex. Although the character system has been extensively studied and its phylogenetic implications revealed in large hymenopterans, e.g. in Aculeata, it remains comparatively understudied in parasitoid wasps. Reductions of character systems due to the small body size in microhymenoptera make it difficult to establish homology and limits the interoperability of morphological data. We describe here the maxillo-labial complex of an ancestral platygastroid lineage, *Sparasion*, and provide an ontology-based model of the anatomical concepts related to the maxillo-labial complex (MLC) of Hymenoptera. The possible functions and putative evolutionary relevance of some anatomical structures of the MLC in *Sparasion* are discussed. Anatomical structures are visualized with Confocal Laser Scanning Microscopy.

Keywords

Mouthparts, Hymenoptera Anatomy Ontology, Confocal laser scanning microscopy, maxillary palpus, labial palpus, galea, lacinia, prementum, glossa

Introduction

Despite relatively recent efforts (e.g., Austin and Field 1997, Murphy et al. 2007), the phylogeny of Platygastroidea remains largely unresolved, as such insights from previously unexplored character systems have the potential to make important contributions to our understanding of the groups evolution. As Platygastroidea are usually reduced

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in body size, the number of informative characters is limited to those anatomical complexes that cannot be simplified without negatively affecting the wasps' survival. In the case of Platygastroidea two character systems seem to match this requirement: the ovipositor apparatus (Austin 1983, Field and Austin 1994, Austin and Field 1997) and the mouthparts including the maxillo-labial complex. While the former is crucial for the piercing the chorion of host egg and laying the wasp's own eggs, the second structure is vital to the process of feeding. Very little is known about the feeding behavior and diet of adult platygastroids. Some species, e.g., the phoretic mantid egg parasitoid *Mantibaria*, feed also on their hosts' body fluids (Clausen 1976).

Due to the extreme diversity of Hymenoptera foraging strategies homologizing mouthpart structures within the order is a challenging task. Other than palpal formulae (Kieffer 1926, Masner 1976, Kononova and Kozlov 2001) and a relatively superficial survey of the maxillo-labial complex (MLC) in some genera of platygastroids (Popovici and Fusu 2006) data on MLC morphology in platygastroids have never been published.

Sparasion is a fairly speciose genus, with 141 valid species (Johnson 1992, Johnson et al. 2008). These wasps are widespread in Eurasia, Africa, and temperate North America (Johnson et al. 2008), and, as far as is known, these species are egg-parasitoids of Tettigoniinae (Orthoptera: Tettigoniidae) (Johnson et al. 2008). Based on the latest phylogenetic analyses, *Sparasion* is part of a small lineage that is sister to either the vast majority of Scelionidae *sensu* Haliday 1839 (Murphy et al. 2007) or Platygastridae *sensu stricto* (Austin and Field 1997). Species in this lineage typically exhibit ancestral morphological states (Murphy et al. 2007, Austin and Field 1997), which should facilitate homologization of mouthparts with other hymenopterans. *Sparasion* are also relatively large species, with less anatomical simplification, which makes them more suitable for dissection and observation.

Material and methods

We examined 34 specimens of 10 *Sparasion* species (Appendix 1). All specimens were stored in 70% ethanol prior to dissection. Card-mounted voucher specimens are deposited in the Insect Collection of University "Al.I.Cuza" Faculty of Biology, Iasi, Romania (OPPC), in the C. A. Triplehorn Insect Collection, Ohio State University, Columbus, OH, USA (OSUC) and in the Frost Entomological Museum, Pennsylvania State University, State College, PA, USA (PSUC).

We followed the protocols of Prinsloo (1980) for specimen preparation. The head was boiled in 10% phenol in lactic acid for 30 minutes and rinsed in distilled water. The MLC were separated from the cranium using forceps (Dumont #5) and insect pins (size 2), then were transferred into 10% NaOH and macerated for 30 minutes, than transferred and rinsed in glacial acetic acid for 10 minutes. Clear and neutralized MLC specimens were dehydrated using ethanol series (70%, 96%, and 100% alcohol; 30 min each) and transferred to a clove oil droplet on concave microscope slide. The labium was separated from the right and left maxillae and mounted separately in Canada balsam medium.

MLC specimens were examined under Euromex GE 3045 microscope (400×–1000×). Line drawings were made using Reichart drawing tube attached to the same microscope. Photos were taken using a Leica DFC-500 camera mounted on a Leica M 205A stereomicroscope.

CLSM images were taken on glycerin-stored specimens with Zeiss LSM 710 Confocal Microscope. For visualizing anatomical structures we used excitation wavelength of 488 and emission wavelength of 510-680 nm, detected using two channels visualized separately using two pseudocolors (510–580 nm=green; 580–680 nm=red). For visualizing resilin we used excitation wavelength of 405 nm and emission wavelength of 510–680 nm detected using one channel visualized with blue pseudocolor.

For Scanning Electron Microscopy (SEM) specimens were dried using hexamethyldisilazane (HMDS, Brown 1993), mounted on double adhesive tape and coated with gold. SEM images were taken using VEGA T SCAN SEM.

Anatomical concepts used here are defined and aligned with those of Alam 1951, Beutel and Vilhelmsen 2007, Bugnion 1924, 1925, Cockerell 1924, Crampton 1923, Crosskey 1951, Dhillon 1966; Duncan 1939, Eickwort 1969, Forel 1874, Gotwald 1969, Krenn et al. 2005, Liu 1925; Matsuda 1965, Matsuda 1957, McGinley 1980, Michener 1944, Michener 1984, Plant and Paulus 1987, Prentice 1998, Ross 1937, Ritchie and Peters 1981, Ronquist and Nordlander 1989, Snodgrass 1942, Ulrich 1924, Vilhelmsen 1996, Winston 1979 in the Hymenoptera Anatomy Ontology (HAO, Yoder et al. 2010). Anatomical terms in the Results section are linked to the HAO via the URI table (Appendix 2; see Seltmann et al. 2012 for more information about this approach).

Results

Maxilla (integument)

The cardo (cd: Fig. 1A–B) is triangular. The submedial maxillary process of the hypostoma (hys: Fig 1A) inserts submedially on the proximal part of the cardo (caf: Fig. 1B). The mediodistal cardinal ridge, laterodistal cardinal ridge and basal cardinal ridge are present (lcr, mcr, bcr: Fig. 1D) and the inner and outer cardinal processes are absent. The cardo lays almost parallel to the external surface of the hypostoma and is largely obscured by it even if the maxillo-labial complex is fully protracted (Figs 1A, cd: 4A). The conjunctiva connecting the cardo to the rest of the maxillo-labial complex is resilin rich along the stipitocardinal hinge (sch: Fig. 1C).

The stipes is triangular in cross section distally. The posterior stipital wall of the stipes bears the posterior stipital sclerite (pss: Figs 1A, C, 2B, C), while the partly sclerotised medial wall and the convex and membranous anterolateral wall (conj: Fig. 1B) bears the galeo-lacinial complex (Fig. 2A, B, D; gal-lac: Fig. 1B, C). The posterior stipital sclerite is triangular in posterior view, and is margined by the principal carina of stipes (pcs: Figs 1A–C, 3A), which is less rigid and melanized than other regions of the sclerite and is the most developed medially and distolaterally. The principal carina of stipes is equipped

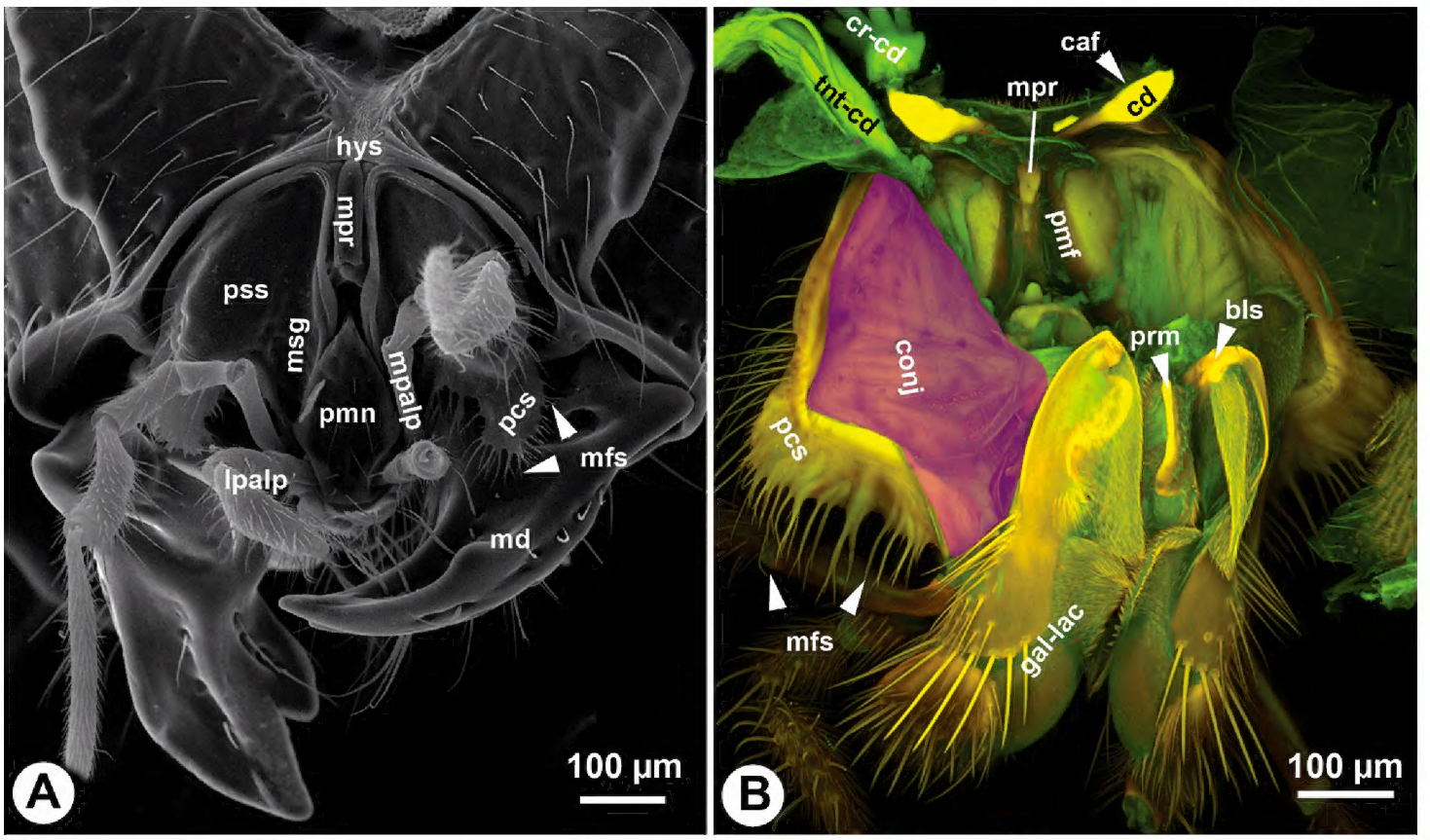


Figure 1. Mouthparts of *Sparasion* sp. **A** SEM micrograph showing the mouthparts, posterior (external) view, distal to the bottom **B** CLSM volume rendered image showing the maxillo-labial complex, anterior (internal) view, distal to the bottom (doi: 10.6084/m9.figshare.861065, doi: 10.6084/m9.figshare.861058) **C** Line drawing showing the maxillo-labial complex, posterior (external), distal to the bottom **D** Bright field image showing the cardo of *Sparasion*, lateral to the left.

distolaterally with the marginal fringe of the stipes (mfs: Figs 1A–C, 2B, C) composed of occasionally branched spines. The extent of the principal carina of the stipes on the distolateral margin is variable in different *Sparasion* species (compare pcs of Fig. 1A with that of Fig. 1B) but it always overlaps the proximomedial surface of the mandible (md: Fig. 1A). The median part of principal carina of the stipes is divided into the proximomedian stipital flange (pmf: Figs 1B, C, 2A) and the distomedial stipital flange (dmf: Figs 1C, 2A, B, C). The proximal part of the distomedial stipital flange posteriorly overlaps the distal part of the proximomedial stipital flange (pmf, dmf: Fig. 1C). The stipes articulates with the postmentum (psm: Figs 1C, 2C) and the distal prementum (pmn: Fig. 1A, C) along the proximomedial stipital flange and with the proximal prementum via the distomedial stipital flange. The medial stipital groove (msg: Figs 1A, 2B) extends medially along the proximomedial stipital flange and distomedial stipital flange and accommodates the first sclerite of the maxillary palp (mpalp: Fig. 1A, C, 3D, E) when it is adpressed against the stipes. The posterior stipital sclerite is glabrous, except a for few, elongate, mechanosensory hairs (msh: Figs 1C, 2B) just proximal of the base of maxillary palp and along the distolateral margin of the stipes abutting the hypostoma. The distal part of the posterior stipital sclerite is equipped with numerous campaniform sensilla (cps: Fig. 2C), which are visible only with transmitted light.

The galeo-lacinial complex has four sclerites and two marginal lobes. The proximal, inverted T-shaped lacinial lever (bls: Fig. 2A, B) and the distal, narrow basal galeal sclerite (bgs: Fig. 2B, D) are situated on the median wall of the stipes and articulate with the posterior stipital sclerite along the distomedial stipital flange. The lacinial bar and lacinial comb are absent. The proximolateral galeal sclerite (pgs: Fig. 2A) is situated in the middle on the lateral wall of stipes and is connected proximally with the lacinial lever and distally with the basal galeal sclerite. The number of mechanosensory hairs in the proximolateral galeal setiferous patch (prs: Fig. 2A) is variable in different *Sparasion* species (Table 1) and overlaps the distolateral galeal sclerite (dgs: Fig. 2A, B, D), which traverses the galeo-lacinial complex and is represented on both its medial and lateral walls (the complex is unilayered at the sclerite). The proximolateral and distolateral galeal sclerites are connected to each other by the lateral galeal crease. The apicomedial galeal plate is absent. The number of setae in the distolateral galeal setiferous patch (dgp: Fig. 2A) is variable in different *Sparasion* species (Table 1). The proximal galeal brush is absent. The single coeloconic sensillum of galea (cfs: Fig. 2B, D) is located distally on the median surface of the distolateral galeal sclerite. The single lacinial lobe (llb: Fig. 2A, B, D) extends anteroproximal whereas the galeal lobe (glb: Fig. 2A, B, D) distal to the proximal galeal sclerites. The lacinial lobe and the proximal part of the galeal lobe are covered with short acanthae (ach: Fig. 2D), which comprise the spiculate patch of the lacinia and the spiculate patch of galea respectively. The galeal comb, galeal lamina and galeal fringe are absent. The velum (vlm: Fig. 2D) is fringed distally in some species (vlm: Fig. 2D). The stipital sclerite is absent from *Sparasion*.

The maxillary palp (1mp: Fig. 2B, D) is connected at the distal apex of the posterior stipital sclerite trough the ventral dististipital process (vdp: Fig. 2B) adjacent to the basal galeal sclerite. The maxillary palp is composed of five maxillary sclerites among

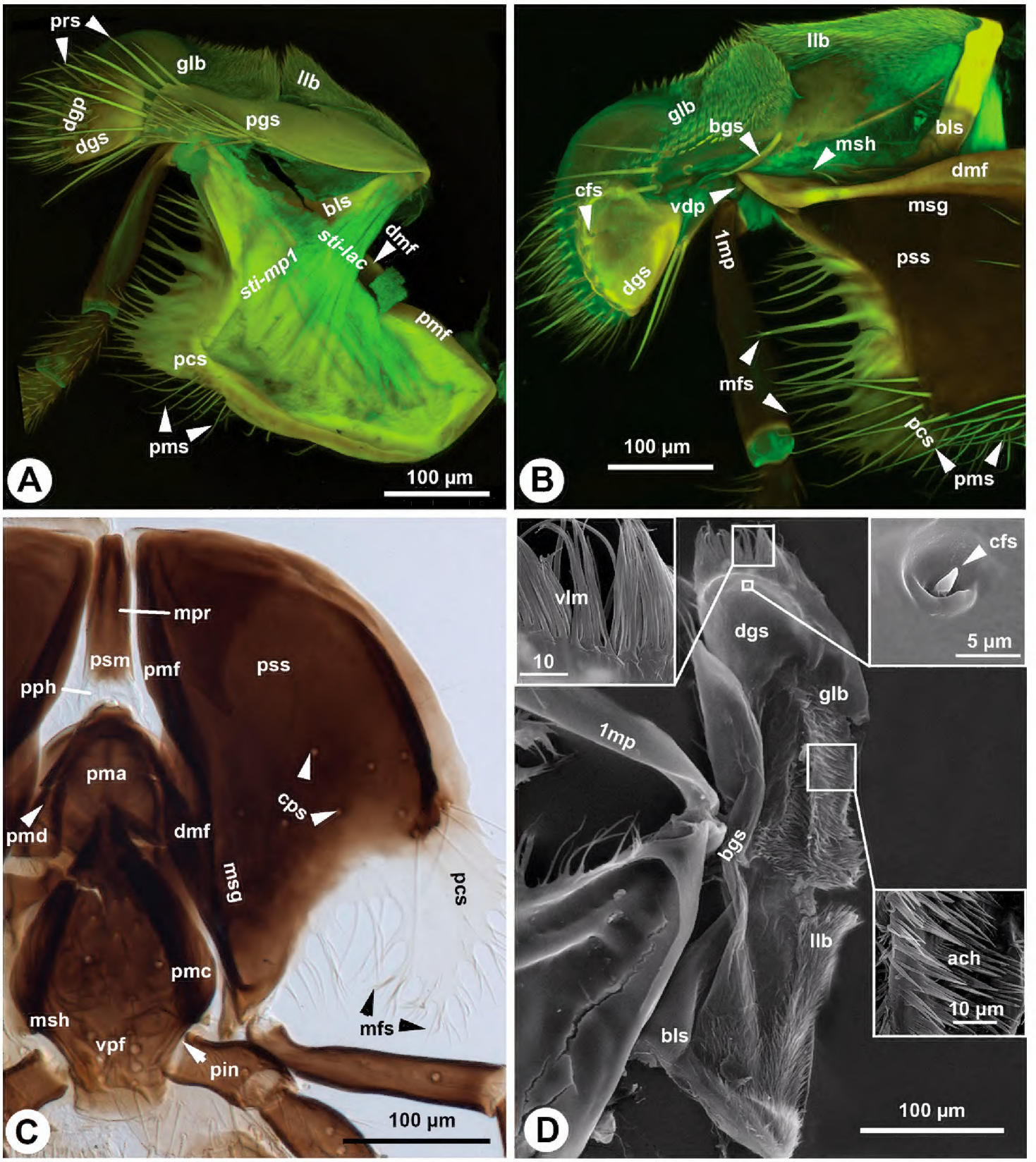


Figure 2. Maxillo-labial complex of *Sparasion*. **A, B** CLSM volume rendered images showing the maxilla: A. anterolateral (internal lateral) view (doi: 10.6084/m9.figshare.861060), distal to the left **B** posteromedial (external medial) view (doi: 10.6084/m9.figshare.861057), distal to the left **C** Brightfield image showing the maxillo-labial complex, posterior (external) view, distal to the bottom **D** SEM micrograph showing the maxilla, posteromedial (external-medial) view, distal to the top.

Table 1.

Characters	*Sparasion*								
	sp.1	**sp.2**	**sp.3**	**sp.4**	**sp.5**	**sp.6**	**sp.7**	**sp.8**	**sp.9**
The number of setae in the proximal galeal brush	5–7	5–7	5–7	5–7	5–7	5–7	7–10	5–7	6
The number of setae in the distal galeal setiferous patch	18–19	18–20	18–20	11–14	18–20	17	27–34	18–20	22
The number of styloconic sensilla on the glossa	14–15	15–16	10–12	10–12	17	23	18–19	15–16	10

which the second sclerite of the maxillary palp is the shortest, and the fifth sclerite of the maxillary palp is always the longest (5mp: Figs 1A,C, 3D, E). The relative width of the maxillary palpal sclerites varies between *Sparasion* species and in some cases even between different sexes (Table 1). Two different setal types can be differentiated on the maxillary palp, based on their gross morphology. The type 1 seta (ss1: Fig. 3B) is a uniporous sensillum whereas the type 2 seta (ss2: Fig. 3B) is a longer mechanosensory hair. A type 1 seta is present on all but the first sclerite of the maxillary palp, which is glabrous in *Sparasion* sp. 4 and sp. 9 and bears only 1–2 type 2 setae in the rest of the species. Type 1 setae are evenly distributed on the third sclerite of the maxillary palp, on the fourth sclerite of the maxillary palp and on the fifth sclerite of the maxillary palp. Type 1 setae are located in 1–4 whorls of setae on the second sclerite of the maxillary palp. Type 2 setae occur only on the third, fourth sclerite of the maxillary palp and on the fifth sclerite of the maxillary palp. The number of type 2 setae is positively correlated with the width of the third sclerite of the maxillary palp and the fourth sclerite of the maxillary palp: type 2 setae are absent from the third sclerite of the maxillary palp if it is not increased in width relative to the second maxillary palpal sclerite.

Maxilla (skeletal muscles)

The *cranio-cardinal muscle* (*cr-cd*: Figs 1B, 4A, B) arises medially of the posterior site of origins of the tentorium and inserts on the cardo just laterally of the cranial fossa of the cardo (caf: Fig. 1B). The *tentorio-cardinal muscle* (*tnt-cd*: Fig. 1B) arises ventrally on the tentorium just laterally of the site of origin of the *tentorio-stipital muscle* (*tnt-sti*: Fig. 4A) and inserts laterally on the stipitocardinal hinge. The tentorio-stipital muscle arises ventrally from the tentorium, medially of the site of origin of the tentorio-cardinal muscle and inserts on the median margin of the posterior stipital sclerite just posterior of the lacinial lever. The *cranio-lacinial muscle* is absent. The *stipito-lacinial muscle* (*sti-lac*: Fig. 2A) arises from along the lateral margin of the posterior stipital sclerite and inserts apically on the lacinial lever. The single *stipito-palpal muscle* (*sti-mp1*: Figs 2A, 3A) and the *stipito-galeal muscle* (*sti-gal*: Fig. 3A) arise medially from the stipito-lacinial muscle, subsequently. The stipito-galeal muscle inserts on the basal galeal sclerite. The *first intrinsic muscle of the maxillary palp*, *third intrinsic muscle of the maxillary palp* and *fourth intrinsic muscle of the maxillary palp* are present, the *second intrinsic muscle of the maxillary palp* was not observed. No muscle was attached to the fifth maxillary sclerite.

Labium, distal hypopharynx (integument)

The postmentum is composed of a single interstipital sclerite that is elongate, rectangular, and is articulated with the posterior stipital sclerites proximolaterally at the proximomedial stipital flange (psm, pmf: Figs 1B, C, 2C). The median postmental ridge (mpr: Figs 1A, B, 2C) is present and the postmental-premental hinge (pph: Figs 1C, 2C) is resilin rich.

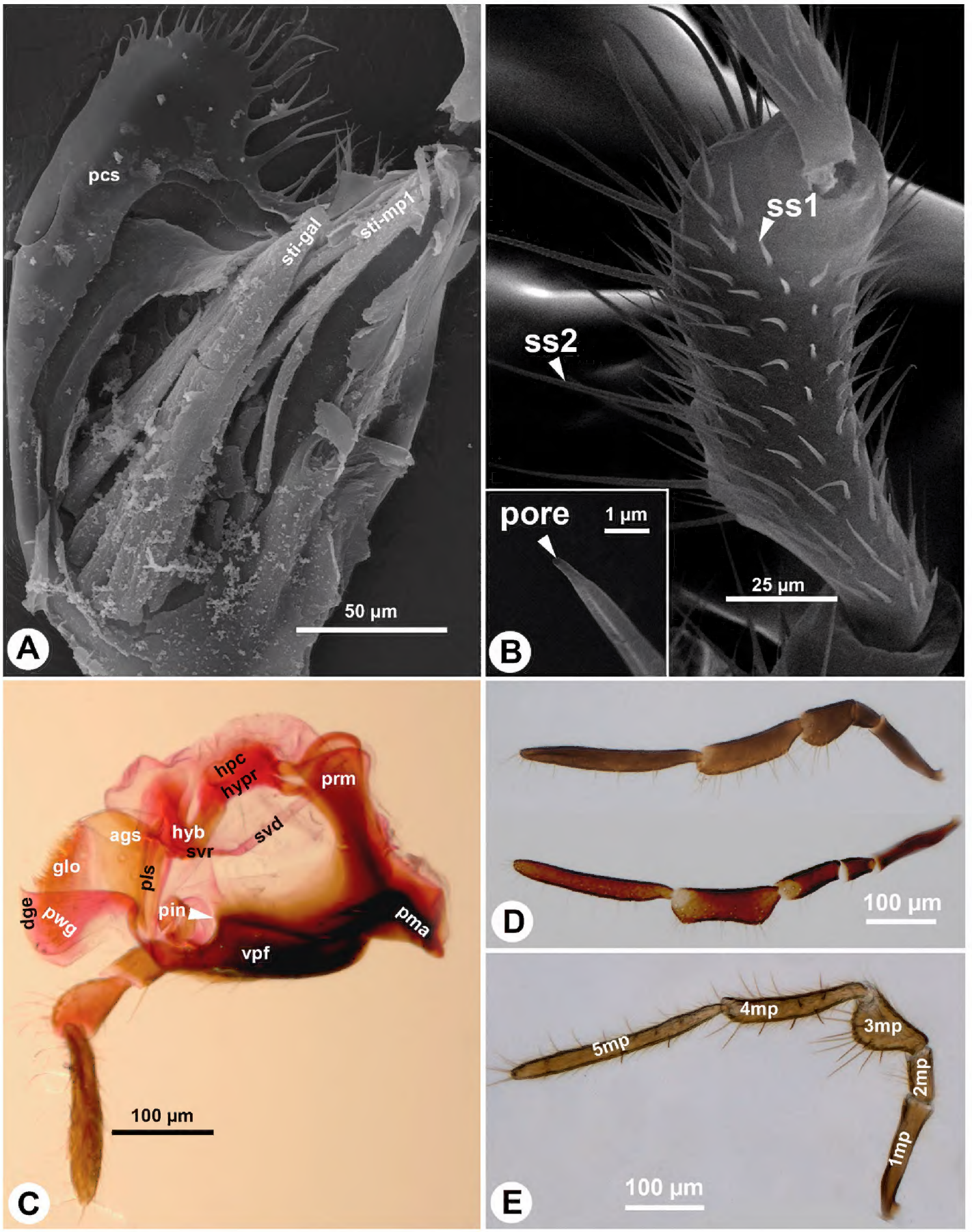


Figure 3. Maxilla and labium of *Sparasion*. **A** SEM micrograph showing the skeletomuscular system of the maxilla, posterior (internal) view, distal to the top **B** SEM micrograph showing the maxillary palp, distal to the top **C** Bright field image showing the labium, lateral view, distal to the left **D, E** Bright field image showing the maxillary palps, distal to the left.

The prementum is connected to the stipes via a conjunctiva (stipito-premental conjunctiva) extending along the proximal margin of the premental arms (prm: Figs 1B, 3C, 4A, B, 5C, 6A–D) and the lateral margin of the prementum proximally of the arm. The

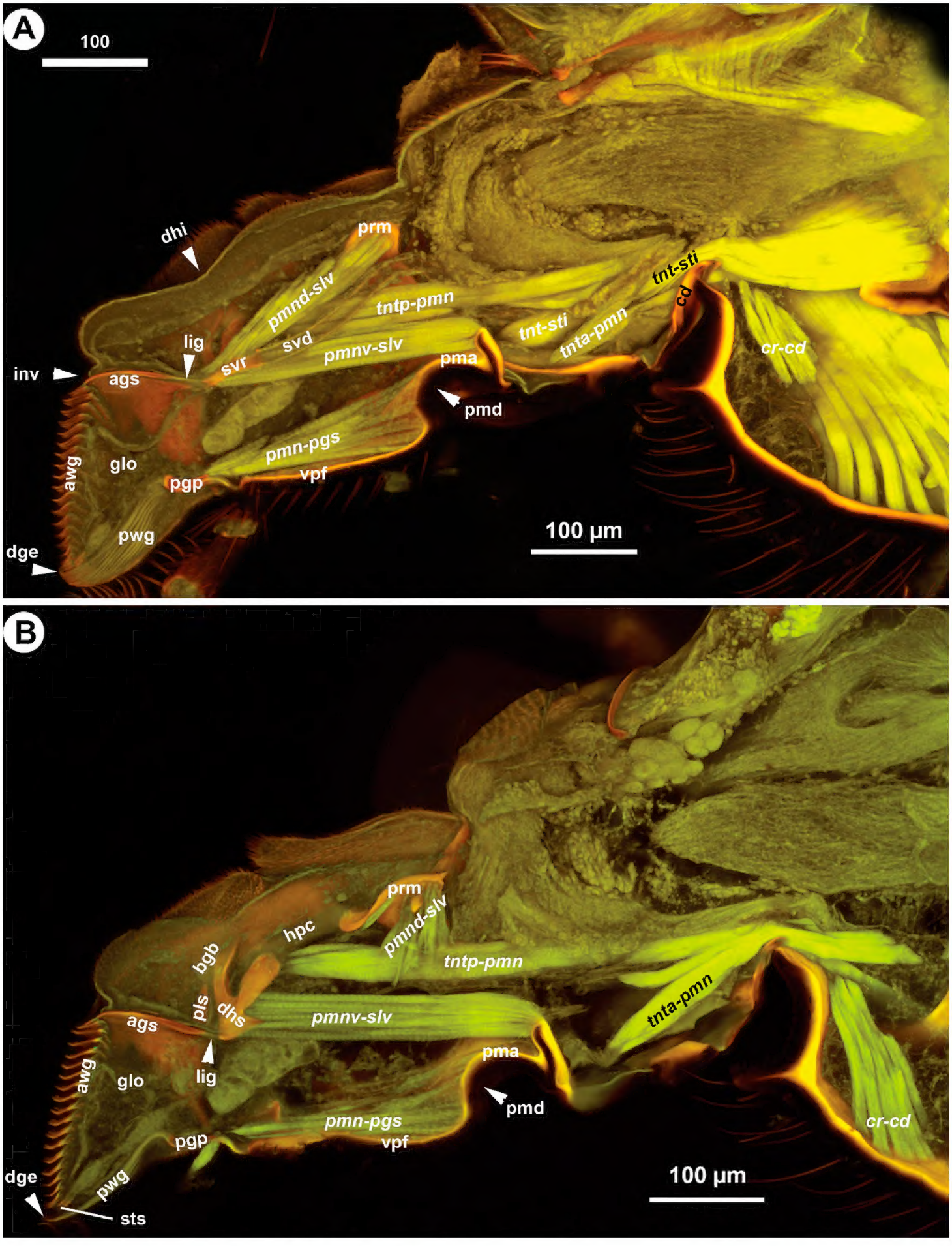


Figure 4. CLSM volume rendered images showing the skeletomuscular system of the labium of *Sparasion*, medial view, distal to the left.

premental carinae (pmc: Fig. 2C and corresponding premental ditches (pmd: Figs 2C, 4A, B, 5C, D, 6A, D) converge proximally and separate the ventral premental face from (vpf: Figs 2C, 3C, 4A, B, 5C, D, 6A, D) the lateral premental face (pma: Figs 2C, 4A, B,

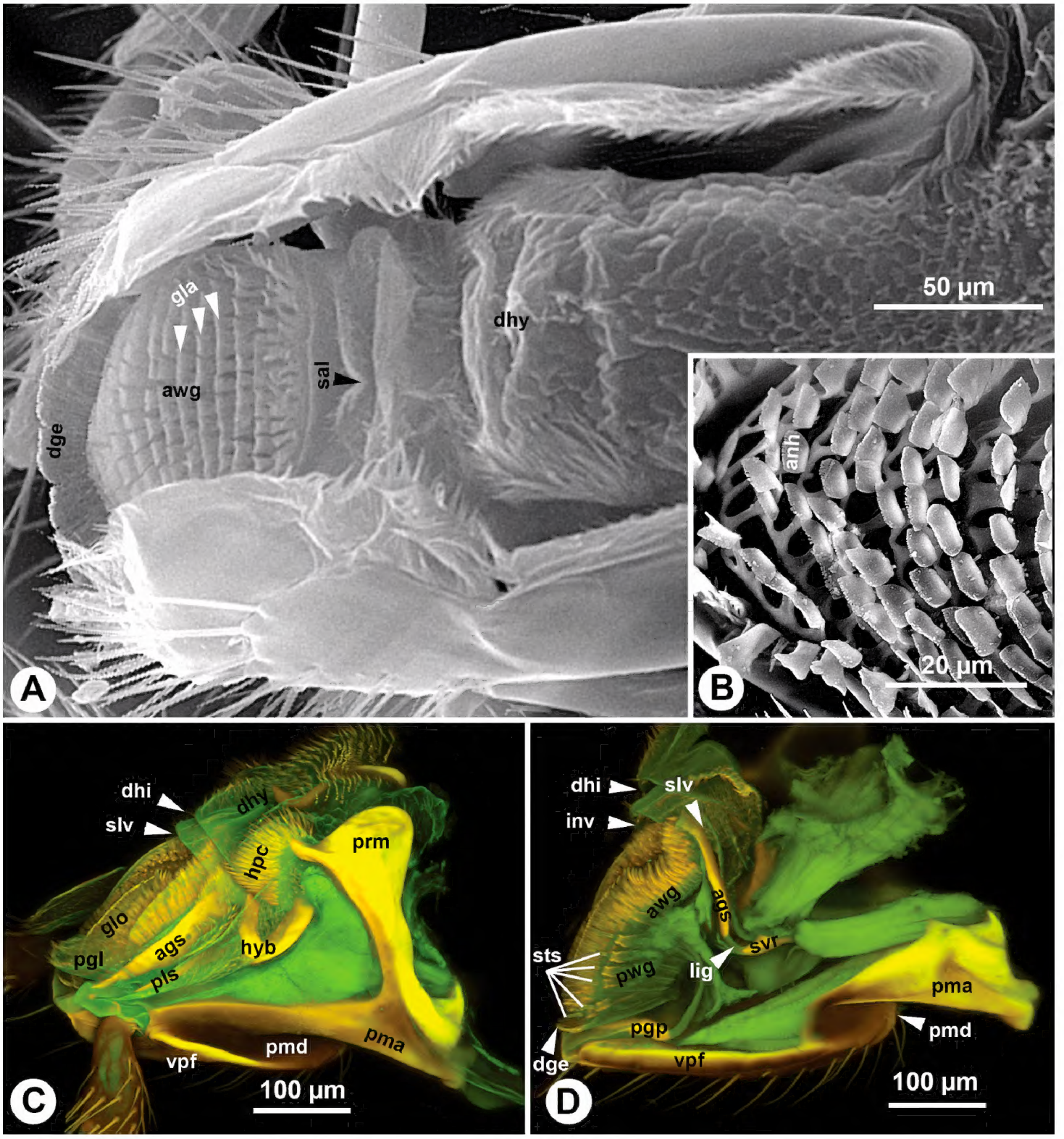


Figure 5. Labium and distal hypopharynx of *Sparasion*. **A** SEM micrograph showing the labium and distal hypopharynx, anterolateral view, distal to the left **B** SEM micrograph showing the glossal annuli, anterior view, distal to the left **C, D** CLSM volume rendered images showing the labium with retracted glossa and paraglossae, distal to the left **C** lateral view (doi: 10.6084/m9.figshare.861064) **D** medial view (doi: 10.6084/m9.figshare.861061).

5C, D, 6A, D). The ventral premental face is flat, diamond-shaped and is equipped with campaniform sensillae of the prementum (cps: Fig. 2C) and distally-oriented mechanosensory hairs (msh: Fig. 2C). The number and pattern of both the campaniform sensilla and mechanosensory hairs and the length of the mechanosensory hairs are variable between different species and sexes (Table 1). The lateral face of the prementum is mostly overlapped ventrally by the distomedial stipital flange (Fig. 1A). The labial palpal excision

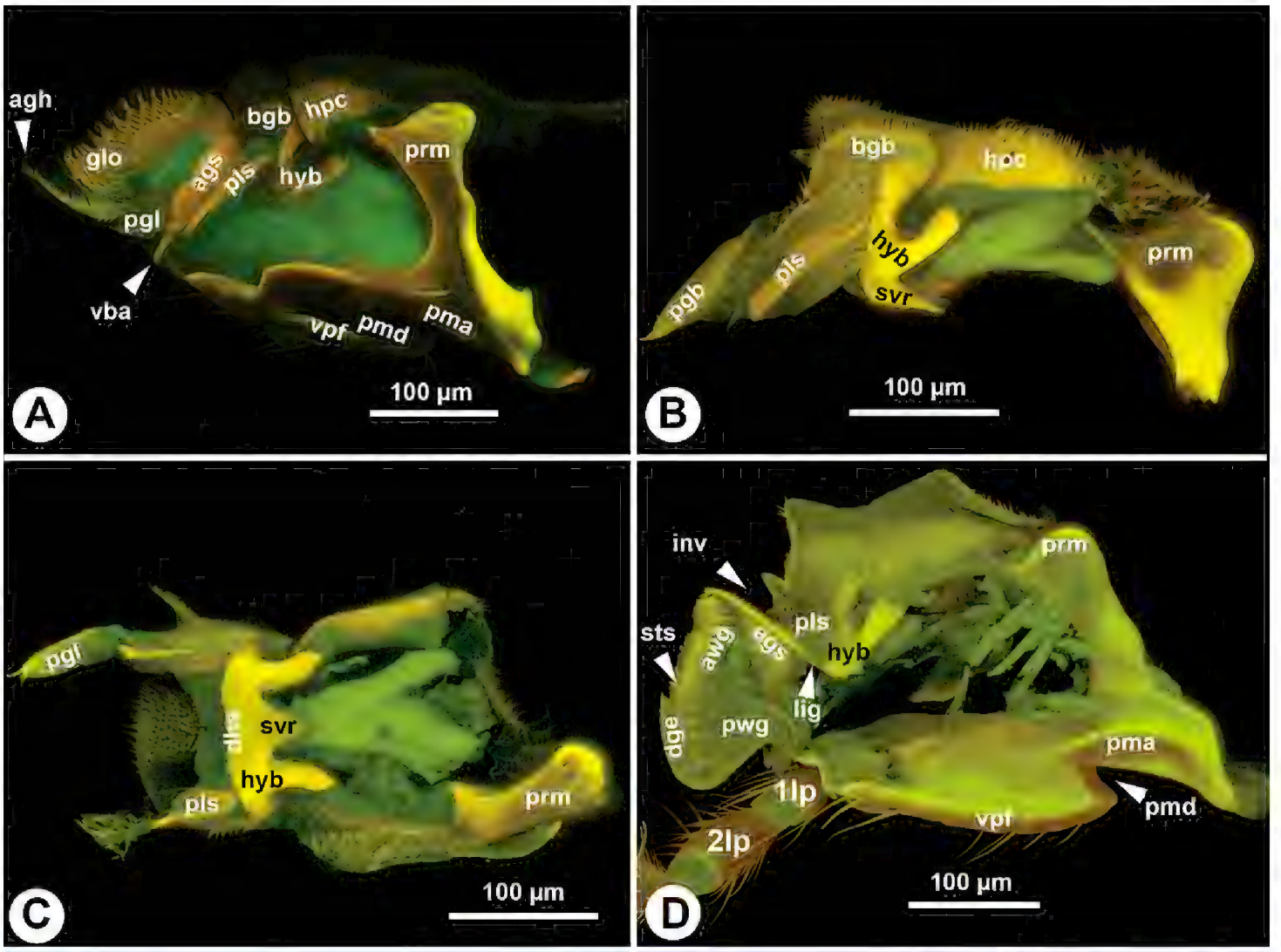


Figure 6. Labium of *Sparasion*. **A** CLSM volume rendered images showing the labium with protracted glossa and paraglossae, lateral view, distal to the left (doi: 10.6084/m9.figshare.861063) **B** CLSM volume rendered images showing the labium, glossa removed, lateral view, distal to the left (doi: 10.6084/m9.figshare.861062, doi: 10.6084/m9.figshare.861066) **C** CLSM volume rendered images showing the labium, glossa removed, posterior view, distal to the left (doi: 10.6084/m9.figshare.861056, doi: 10.6084/m9.figshare.861067) **D** CLSM volume rendered images showing the labium with protracted glossa and paraglossae, medial view, distal to the left (doi: 10.6084/m9.figshare.861059) **E, F** Bright field images showing the labium, posterior view, distal to the top.

(pin: Figs 2C, 3C) accommodating the base of the labial palp is distinct on the disto-lateral corner of the prementum. The labial palp is composed of three sclerites that are equipped with both the uniporous sensilla (type 1) and mechanosensory hairs (type 2).

The glossa (glo: Figs 1C, 3C, 4A, B, 5C, 6A) is separated anteroproximally from the paraglossae (pgl: Figs 5C, 6A, C) and the distal hypopharynx by the basal glossal invagination (inv: Figs 4A, 5D, 6D) adjacent to the salivarium (svr: 6B, C, F). The anterior glossal sclerites (ags: Figs 3C, 4A, B, 5C, 6A, D) are embedded into the distal wall of the invagination and are connected medially to the ventral wall of the salivarium via a ligament (lig: Figs 4A, B, 5D, 6D). The ventrolateral basiglossal arms are distinct (vba: Fig. 6A, F) and each anterior glossal sclerite is equipped with a single campaniform sensillum of the glossa (csg: Fig. 6F). The posterior glossal plate is composed of a single, median sclerite (pgp: Figs 4A, B, 5D, 6E, F). The flat posterior surface of the glossa (pwg: Figs 3C, 4A, B, 5D, 6D) is glabrous with distinct ventral glossal lines. The distal glossal edge (dge: Figs 3C, 4A, B, 5A, D, 6D) is thicker than the proximal region of the posterior surface of the glossa. The apical glossal hairs are usually present (agh: Fig. 6A). The apical glossal setae (sts: Figs 5D, 6D, E) are styloconic sensilla with variable number in different species (Table 1).

The arched anterior surface of the glossa (awg: Figs 4A, B, 5A, D, 6D) is evenly covered with glossal annuli (gla: Fig. 5A), which are composed of transverse rows of spatulate and anteriorly curving annular hairs, each with a dentate distal margin (anh: Fig. 5B).

The bilobed paraglossae arise proximolaterally of the basal glossal invagination and encircle the proximal part of the glossa. The elongate, triangular basiparaglossal sclerite (pls: Figs 3C, 5C, 6A–D, F) corresponds to a posterior lobe of the paraglossa whereas the larger anterior lobe of the paraglossa bears the distal, less sclerotised paraglossal acroglossal button (pgb: Fig. 6B). Proximally the paraglossa is continuous with the wall of the distal hypopharynx (dhy: Fig. 5A, C) and the paraglossal sclerite is connected to the distal hypopharyngeal sclerite via an elongate ligament. The basiparaglossal brush (bgb: Figs 4B, 6A, B, F) is distinct but the paraglossal sclerite and paraglossal annuli are absent.

The distal hypopharynx is supported laterally by the premental arms and the hypopharyngeal rod (hypr: Fig. 3C), which is continuous with the distal hypopharyngeal sclerite via the hypopharyngeal button (hyb: Figs 3C, 5C, 6A–D). The hypopharyngeal pecten (hpc: Figs 4B, 5C, 6A, B) is distinct and abuts the basiparaglossal brush when the ligula is retracted (hpc: Figs 5C). The hypopharyngeal buttons are connected to each other medially trough the ventral wall of the salivarium, that is either sclerotised (svr: Figs 3C, 6B; salivarial sclerite) or is a resilin rich conjunctiva (svr: Fig. 6F). In the former case the hypopharyngeal buttons and the ventral, sclerotised wall of the salivarium compose the distal hypopharyngeal sclerite (dhs: Figs 4B, 6C) encompassing ventrally the salivary duct (svd: Figs 3C, 4A). The distal hypopharyngeal invagination (dhi: Figs 4A, 5C, D) corresponds to the dorsal bend on the hypopharyngeal button.

Labium, distal hypopharynx (skeletal muscles)

The *postmento-premental muscle* is absent. The *posterior tentorio-premental muscle* (*tntp-pmn*: Fig. 4A, B) arises from the tentorium anterolaterally from the site of origin of the *anterior tentorio-premental muscle* (*tnta-pmn*: Fig. 4A, B) and inserts on the proximal part of the hypopharyngeal button. The *anterior tentorio-premental muscle* arises from the tentorium medially of the site of origin of the posterior *tentorio-premental muscle* and inserts proximomedially on the postmental-premental hinge. The *premento-paraglossal muscle* (*pmn-pgs*: Fig. 4A, B) arises medially from the internal edge corresponding to the premental ditch and from the intima of the median premental face anterior to the edge and inserts on the posterior glossal plate. The *dorsal premento-salivarial muscle* (*pmnd-slv*: Fig. 4A, B) arises distomedially from the premental arm and inserts dorsally on the salivarium. The *ventral premento-salivary sclerite muscle* (*pmnv-slv*: Figs 4A, B) arises from the proximal premental area and inserts proximomedially on the distal hypopharyngeal sclerite. The *premento-palpal muscle* arises anterolaterally from the site of origin of the premento-paraglossal muscle. The *first intrinsic muscle of the labial palp* and the *second intrinsic muscle of the labial palp* are present. The premento-glossal muscle is apparently absent.

Discussion

The maxillo-labial complex of *Sparasion*

The term maxillo-labial complex (MLC) is used by Snodgrass (1935). However, many entomologists prefer to use the term labio-maxillary complex, e.g. Duncan (1939), Labandeira (1997), Jervis (1998), Vilhelmsen (1996), Krenn (2007). The reason for using the latter seems to be that it is more easily pronounced (Duncan 1939). In this paper the term maxillo-labial complex is preferred because it corresponds with the anatomical position of the component pieces.

The hymenopteran labium, unlike that of other holometabolan insects, is so tightly connected to the maxillae by the labiomaxillary hinge that they protract and retract together as a single unit (Duncan 1939, Snodgrass 1942, Vilhelmsen 1996, Krenn 2007). While the labiomaxillar hinge connects their proximal parts, the distal, more sclerotised regions of the maxillae and the labium still are able to move with some freedom in basal Hymenoptera (Vilhelmsen 1996, Beutel and Vilhelmsen 2007) and in a few apocritan taxa (e.g. in *Gasteruption*, *Evania* (Evanioidea) (Fig. 8) and *Gryon* (Platygastroidea) Mikó, pers. obs.). However, in *Sparasion* and some other apocritan taxa (*Ibalia* (Cynipoidea) Ronquist & Nordlander, 1989, *Vespula* (Vespoidea) Duncan, 1939) where the posterior wall of the labium and maxilla are almost exclusively sclerotised, the freedom of the independent movement between the appendages is restricted: they can not be separated from each other and sometimes – e.g. in *Sparasion*

— not even from the hypostoma. The development of rigid connections between sclerites that are flexibly connected in basal Hymenoptera seems to be an apocritan evolutionary trend, which is arguably related to their more sclerotised body (Vilhelmsen 2000a, 2000b, Vilhelmsen et al. 2010).

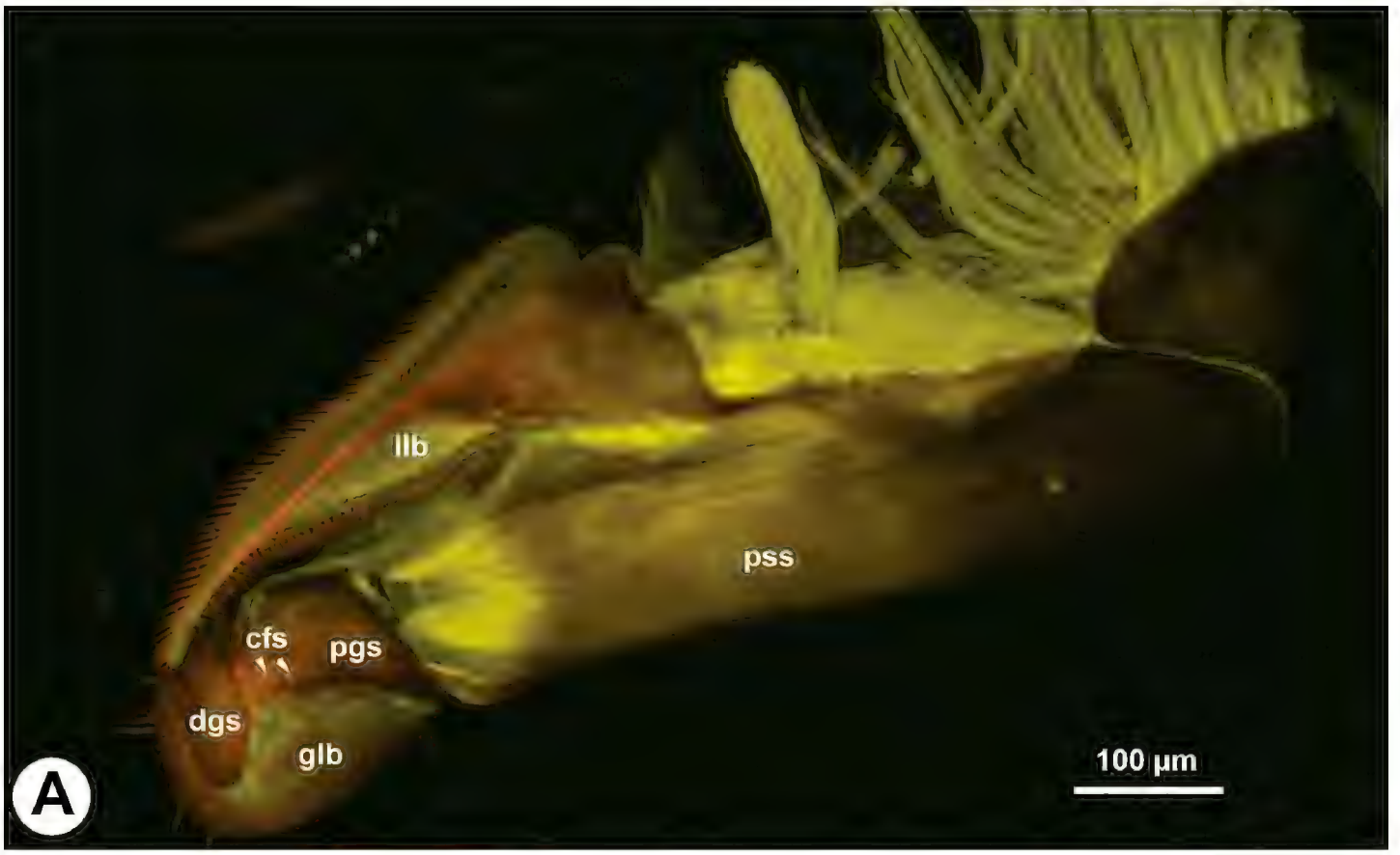
Although the MLC of *Sparasion* is reduced in size and highly sclerotized, we were able to homologize most of its anatomical structures to those of other Hymenoptera (Appendix 2, Figs 7–9). We hypothesize that the platygastroid MLC is an anatomical system with enough phenotypic diversity to serve as a source of morphological characters for phylogenetic analyses and species diagnosis.

Maxilla

One consequence of the more heavily sclerotised and less moveable MLC is that the cardo remains relatively simple in *Sparasion*, retaining its main function: providing rigid attachment of the MLC to the cranium. The inner and outer processes of the cardo (Winston 1979) that articulate with the stipes are missing from *Sparasion*, similarly to other Proctotrupomorpha (e.g., *Ibalia* and *Pelecinus* pers. obs.). Because the stipito-cardinal articulation is absent, the cardo seemingly interacts with the posterior stipital sclerite only by the resilin rich stipito-cardinal hinge. Similarly to *Sparasion*, the cardo is not visible externally in these taxa and even if the MLC is in a protracted position, the cardo is obscured by the proximal portion of the principal carina of the stipes.

Different levels of sclerotization can be observed on the intercardinal and interstipital areas in different hymenopteran taxa. Only the intercardinal area contains a sclerite in basal Hymenoptera (Ross 1937), while both intercardinal or interstipital sclerites may be present in Apocrita. The intercardinal and interstipital areas are separated from each other by the labial suture (Snodgrass 1935, Prentice 1998). The median area of the MLC posterior to the suture contains an anterior and a posterior sclerite in some holometabolan insects (i.e. Coleoptera), the submentum and the mentum. This condition never occurs in Hymenoptera (see references listed in materials and methods section). Even in those Aculeata where two medial sclerites are in the postmental area, one is always anterior to the labial suture. Based on the their position relative to the stipites and cardines, the intercardinal postmentum of basal Hymenoptera might be homologous with the postmentum in other insects and the interstipital postmentum of Apocrita is most likely not homologous to these structures. The postmental area is fully membranous in many Apocrita (*Evania*, psm: Fig. 8; *Vespula*, Duncan 1939; *Stenobracon*, Alam 1951). Only the intercardinal sclerite is present in *Ibalia* (Ronquist and Nordlander 1989) leading Ritchie and Peters (1981) to homologize this structure with the mentum of other holometabolans.

Only the interstipital postmentum (Prentice 1998) is present in *Sparasion*. This sclerite is not connected with muscles, nor is it articulated with any other sclerites. It's only function might be to separate the posterior stipital sclerites from each other.



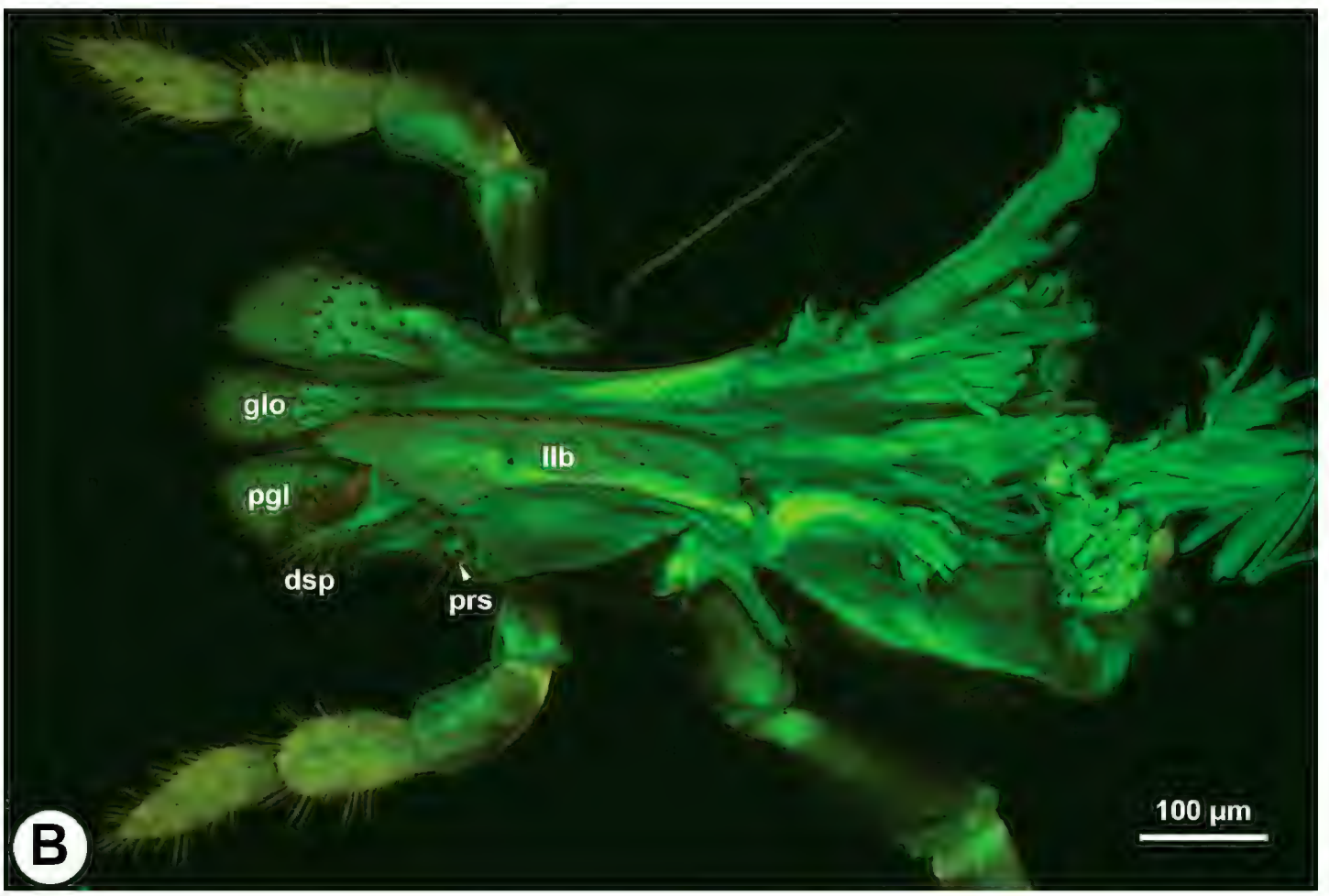


Figure 7. CLSM volume rendered images showing the MLC of *Athalia rosae*. **A** maxilla, medial view, doi: 10.6084/m9.figshare.956279 **B** MLC, anterior view, distal to the left, doi: 10.6084/m9.figshare.956279

The development of the principal carina arguably correlates with the presence of rigid connection between the stipes and neighboring sclerites. In those taxa, where the stipes articulates with the hypostoma, but not with the labium, the principal carina is present only laterally (*Evania*, pcs: Fig. 8).

Figure 8. CLSM volume rendered image showing the mouthparts of *Evania* sp, posterior view, distal to the bottom, doi: 10.6084/m9.figshare.956280

Both the medial and lateral portions of the carina are well developed in *Sparasion*, having two unique characteristics that were not found in other Hymenoptera (see references listed in the materials and methods section):

1. The median portion of the carina is divided into two sections that overlap each other and accommodate the proximal and distal part of the lateral premental margin.
2. The presence of an "apical fringe", a branched flattened evagination along the distolateral margin of the carina. While the first specialization might be the consequence of the articulation between the posterior stipital sclerite and the prementum, the second is most probably related to the unique movement of the mandible in *Sparasion*. While pivotal axis of the mandible is anteroposterior in most Hymenoptera taxa (dorsoventral in a prognathous head) it is directed medi-

Figure 9. CLSM volume rendered image showing the maxilla of *Orthogonalys pulchella*, posteromedial view, distal to the top-left, doi: 10.6084/m9.figshare.956281

olaterally in *Sparasion* and the mandibles are moved parallel to the body axis (Mikó et al. 2007). Due to this unique, oblique position of the mandible, the distolateral, fringed margin of the principal carina is positioned inside the internal concavity of the mandible and seemingly acts as a cleaning "brush". Similar movement of the mandible has been reported from many other Hymenoptera taxa, including

two platygastrid genera, *Tyrannoscelio* and *Encyrtocelio*. It would be worthwhile to study the MLC of these taxa and to clarify whether the fringed lateral portion of the principal carina is unique for *Sparasion* or whether it can be found in other genera with modified mandible movement.

The presence of the campaniform sensillum of the stipes was considered as one of the synapomorphies of the clade composed of Platygastroidea and Cynipoidea (Sharkey et al. 2012). Although the sensillum is present in *Sparasion* and some other platygastrid taxa (Sharkey et al. 2012), it is absent from *Triteleia*, *Calliscelio*, *Macroteleia*, *Apegus*, *Duta*, *Psilanteris*, *Anteris* (Popovici and Fusu 2006), which implies that this character might be useful for generic classification in Platygastroidea.

Prentice (1998) reported the presence of two apical sclerites on the galea, the apicolateral and apicomedial stipital plates. We were able to locate only one apical sclerite, the distolateral galeal sclerite on the galeo-lacinial complex of *Sparasion*. This sclerite traverses the complex and bears both the distolateral galeal setiferous patch and the medial coeloconic sensillum that define the apicolateral and apicomedial stipital plates respectively.

Appendage segments and annuli are ring-like and repetitive sclerites of the legs, antenna, labial palps and maxillary palps. While appendage segments have muscles attaching to them, annuli do not. Annuli are traditionally differentiated from appendage segments by names with the suffix "-mere" e.g. flagellomere and tarsomere. Among the five maxillary palpal sclerites of *Sparasion* the fifth one does not have muscle attachments. We observed a similar condition in *Orthogonalys* (Trigonalidae), where the fifth and sixth sclerites lack any muscle attachment (Fig. 9). If we apply the annuli vs. segment terminology system to these taxa, we should call the first four sclerites "palpal segments" and fifth sclerite in *Sparasion* and the fifth and sixth sclerites in *Orthogonalys* "palpomeres". To avoid misinterpretations of the segment identity of the palpi, and keeping a simple and easily applicable terminology we prefer to use palpal sclerites for the ring-like sclerites of the palpi.

Sparasion has five maxillary palpal sclerites that is the highest in Platygastroidea (Masner 1976). Since the presence of five maxillary palpal sclerites is a possible synapomorphy for Proctotrupomorpha (Sharkey et al. 2012), and is also shared by other, putatively basal lineages of Platygastroidea (i.e. *Archaeoteleia*, *Nixonia* and *Plaumannion*, Johnson et al. 2008) it is most probable that this condition is plesiomorphic for Platygastroidea.

The maxillary palp is located medially on the lateral margin of the posterior stipital sclerite in basal Hymenoptera distantly from the apical end of the sclerite bearing the base of the galea (Fig. 7B., Vilhelmsen 1996, Beutel and Vilhelmsen 2007). In *Sparasion* the palp is connected to the apical vertex of the posterior stipital sclerite, adjacent to the base of the galeo-lacinial complex. This distal position makes it difficult to interpret the presence of minute anatomical structures such as the palpifer ("flexible and transparent, very difficult to detect structure" at the base of the maxillary palp, Prentice 1989).

The 2nd, 3rd and 4th maxillary palpal sclerites are distinctly wider than the more proximal or distal maxillary palpal sclerites in some *Sparasion* species (Figures 3D, E).

The number and position of these modified sclerites are sexually dimorphic in some *Sparasion* species and are seemingly useful for species groups definitions. A widened 4th palpal sclerite was found in most species of the plesiomorphic platygastrid genus *Nixonia*, and representatives of *Plaumannion*, *Archaeoteleia*, *Sceliomorpha* and *Neuroscelio* (Johnson and Masner 2006, Johnson et al. 2008); the presence of enlarged 3rd maxillary palpal sclerites have been reported from *Sparasion* (Johnson et al. 2008) and enlarged 2nd and 3rd sclerites from the putatively most primitive extant platygastroid genus, *Huddlestonium* (Masner et al. 2007).

Although the position of enlarged palpal sclerites in the maxillary palp has often been used for the classification of different Hymenoptera taxa (i.e. Evaniidae, Deans and Huben 2003; Aculeata, Bohart and Menke 1976), our knowledge about their possible function is rather incomplete. Albeit our study confirms Prentice's (1998) observation that enlarged sclerite size corresponds to larger muscle mass, the role of this modification in the mechanics of palpal movement is still unrevealed.

Although the presence of only two stipito-palpal muscles is considered as the Hymenoptera groundplan (stia-mp1, stip-mp1: Fig. 9; Beutel and Vilhelmsen 2007), similarly to *Sparasion*, only one maxillary plapal muscle has been reported from many Hymenoptera taxa (Snodgrass 1942, Matsuda 1957, Prentice 1998). The presence of resilin-rich conjunctiva at the base of the maxillary palpus in *Sparasion* supports Prentice's hypothesis that the expansion of the maxillary palpus is facilitated by a resilin rich region between the posterior stipital sclerite and the palpus in taxa with a single stipito-palpal muscle.

The terms, galea and lacinia refer usually to the evaginated distal, sclerotised regions of the maxillar cuticle that are adjacent to the sites of insertions for the stipito-lacinial, cranio-lacinal and the stipito-galeal muscles in insects. Although these muscles are present in most hymenopterans (sti-gal, sti-lac: Fig. 7A, and more proximal and more distal lobes can almost always be differentiated, the proximal limits of the galea and lacinia are difficult to define and thus these structures are difficult to homologize to that of other insects where the galea and lacinia are well sclerotised. Therefore we preferred to use galeal lobe and lacinial lobe instead of galea and lacinia in the present paper.

Two distinct setiferous areas can be defined on the lateral area of the galeal lobe in *Athalia*: a proximal row of setae traversing the galea (prs: Fig. 7B) and a more distal setiferous patch (dsp: Fig. 7B). The presence of these two setiferous areas seems to be consistent within Hymenoptera (Prentice 1998) and can be used for the delimitation of areas of the galeo-lacinial complex.

In *Sparasion*, similarly to some other, more derived Hymenoptera taxa these setiferous areas correspond to two sclerites, the proximolateral and distolateral sclerites of the galea (Prentice 1998, Ronquist and Nordlander 1989). Two distal sclerites are located on the medial wall of the galeo-lacinial complex in *Athalia* (pgs, dgs: Fig. 7A), with some campaniform sensillae (cfs: Fig. 7A). Based on the presence of the sensilla on the medial wall of the distal galeal sclerite of *Sparasion* it is possible that the distal galeal sclerite, or at least its medial part (the sclerite traverses the galeo-lacinial complex) is homologous with one of the apical galeal sclerites of *Athalia*.

Although the velum is well developed in numerous other Hymenoptera (Prentice 1998), we are not aware of any case in the order where the lobe is fringed apically as it was found in some *Sparasion* species (vlm: Fig. 2D).

The galeal comb and the galeal lamina are important characters that have been used in aculeate systematics (Prentice 1998, "comb of galea" in Michener 1944, "Borstenkamm" in Ulrich 1924). Although neither of these structures are present in *Sparasion*, they are present in some other scelionines (*Encyrtoscelio*, *Teleas*, *Trimorus* Popovici pers. obs.).

Labium

The prementum is articulated with the stipes via the premento-stipital articulation that is composed of the premental ditch, premental carinae, and the principal carina of the stipes. Duncan (1939) reported a similar connection between the stipes and the prementum and considered its importance in the simultaneous movement of these two structures. Although we are unaware of other hymenopterans with a complete premento-stipital articulation, the premental carinae are present in some Evaniidae (pmc: Fig. 8) and in some platygastroid genera (illustrations in Popovici and Fusu 2006).

Vilhelmsen (1996) proposed the presence of acanthae on the hypopharyngeal rod as a possible synapomorphy for Apocrita. In *Sparasion* and in some other apocritans (e.g. *Vespula*, Duncan 1939; in Apoidea, =spiculate patch of the hypopharynx in Prentice 1989, *Evania* pers. obs.) two regions of the hypopharyngeal rod, the hypopharyngeal pecten (hpc: Fig. 10) and the basiparaglossal brush (bgb: Fig. 10) are extensively covered with acanthae. Contraction of the posterior tentorio-premental muscle might protract, whereas contraction of the ventral premento-salivarial muscle retract the hypopharyngeal buttons. The distal hypopharyngeal invagination, which is apparently unique for Platygastroidea, is defined by the hypopharyngeal button. Protraction and retraction of the button, therefore, might actually control the orientation of the invagination. We were not able to locate an infrabuccal pouch (Fig. 10) in *Sparasion* between the transverse line connecting the tips of the lateral arms of the prementum and the sitophore in basal Hymenoptera (Vilhelmsen 1996).

The maximum number of labial palpal sclerites in Apocrita is four (some Formicidae (Gotwald, 1969), Braconidae (Belokobylskij, 2006), Vespinae (Duncan, 1939)). In *Sparasion*, the labial palp is composed of three sclerites that are moved directly by muscles. In those Hymenoptera where the labial palp is composed of four sclerites (Vilhelmsen and Beutel 2007, Gotwald 1969, Belokobylskij and Chen 2006, Duncan 1939) the apical sclerite has no muscles and is considered to be a secondary subdivision of the apical segment. The presence of four labial palp sclerites is considered a hymenopteran synapomorphy (Vilhelmsen and Beutel 2007) and the ground plan of almost all other apocritan superfamilies (Sharkey et al. 2012). The ground plan of a three-segmented labial palp of Platygastroidea is probably the result of the secondary loss of the apical palpal sclerite.

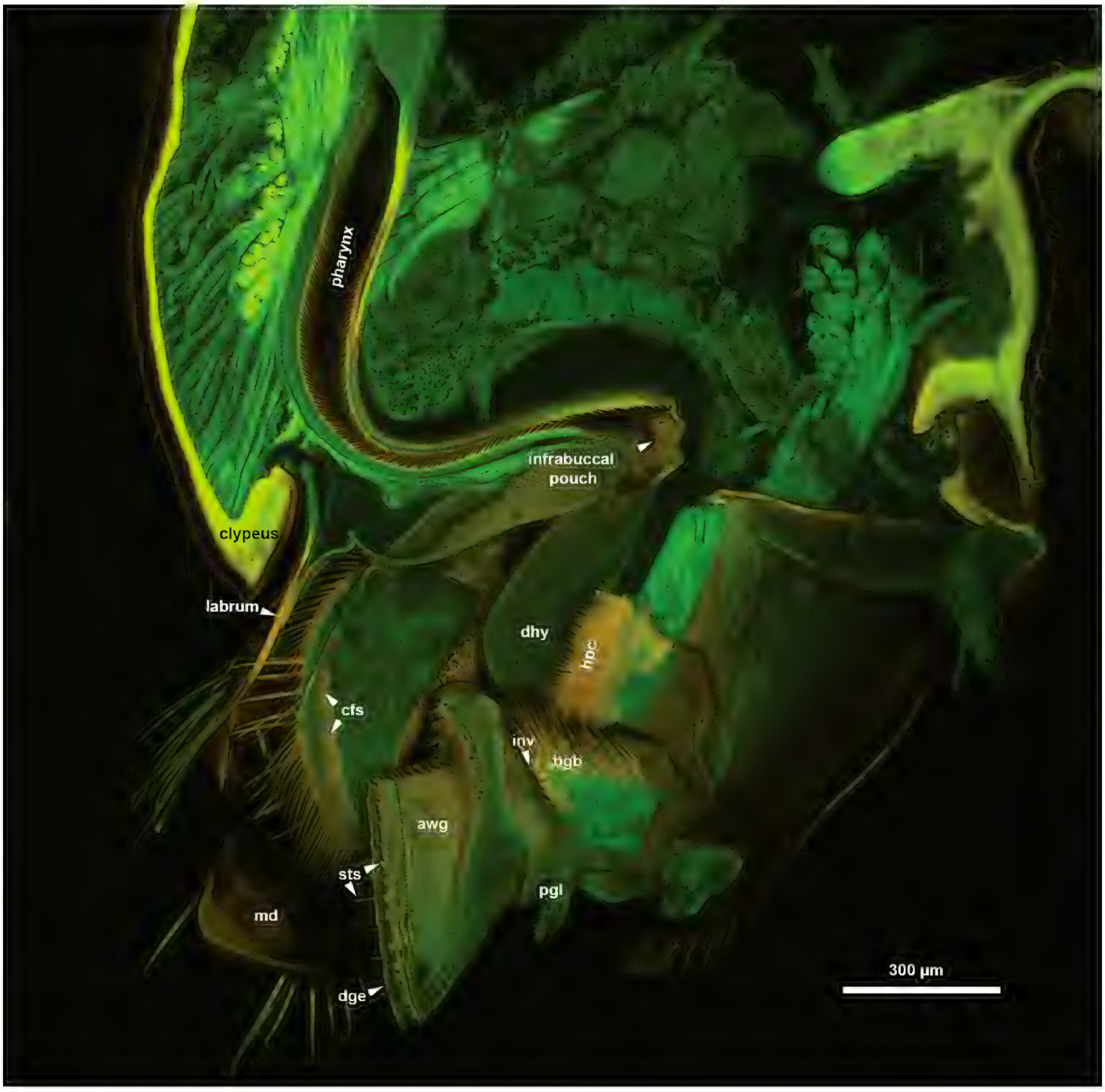


Figure 10. CLSM volume rendered image showing the ventral region of the head of *Evania* sp., medial view, distal to the bottom, doi: 10.6084/m9.figshare.956282

Duncan (1939) hypothesized that the glossal annuli have rasping function or are involved in retaining liquids in Vespinae. Glossal annuli with elongated and well developed spatulate annular hairs are present in most Apocrita (Duncan 1939, Prentice 1998, Ronquist and Nordlander 1989, Dangerfield et al. 2001, Popovici and Fusu 2006) while are present only in a few basal Hymenoptera taxa (Cephoidea, Megalodontoidea and Orussioidea, Vilhelmsen 1996).

Along the proximal margin of distal edge of glossa in *Sparasion*, a row of 9–23 apical glossal setae can be observed. These setae are styloconic sensilla, which are considered to be bimodal contact chemo-mechanosensillae (Shields 2010). Although they have never been mentioned elsewhere, these styloconic setae are present in other Hymenoptera (*Evania*, sts: Figs 8, 10, *Gasteruption*, *Ibalia*, Mikó pers. obs.) and might play crucial role in the chemo- and mechanosensation in Apocrita.

The ventral glossal lines have been reported only from a few Hymenoptera (Salman 1929, Prentice 1998, *Evania*, Fig. 8). The lines radiate from the posterior glossal plate and extend toward the apical glossal hairs and therefore might be related to the presence of these styloconic sensilla. We have found the lines present in taxa whith apical styloconic sensilla.

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Appendix 1

Specimens examined.

Taxon	Number of specimens	Data labels
Anteris sp.	1	ROMANIA: Botosani, 10.viii.2004, leg. O. Popovici
Anteris sp.	1	ROMANIA: Iasi, 26.vi.2004, leg. O. Popovici
Apegus sp.	1	ROMANIA: Iasi, 30.vi.2004, leg. O. Popovici
Athalia rosae	1	Wildtype culture, 2005, M. Hatakeyama
Belyta sp.	2	ROMANIA: Iasi, 10.ix.2005, leg. O. Popovici
Calliscelio sp.	1	ROMANIA: Bacău, 31.viii.2002 , leg. O. Popovici
Calliscelio sp.	1	ROMANIA: Holboca (Iaşi), 30.06.2002, leg. I. Moglan
Duta sp.	1	ROMANIA: Bacau, 17.vii.2004, leg. O. Popovici
Evania sp.	2	Costa Rica, 21.II.2005 15/M/16/016 1500-site Costa Rica Heredia, 9km NE Vara Blanca, 10°14'N (INBIO)
Gasteruption sp.	2	USA WV, Hardy Co., 11–22.v.2006, MT, D. Smith
Ibalia sp	1	USA: Virginia, Fairfax Co., Great Falls, 18–30.v. 2007, leg. D. Smith
Ibalia sp	1	USA: Motgomery Co., 21.v. 2010, leg. N. E. Woodley
Ibalia sp.	1	USA: Virginia, Fairfax Co., Great Falls, 31.v.-13.vi.2007, leg. D. Smith
Macroteleia sp.	1	ROMANIA: Iasi, 17.viii.2004, leg. O. Popovici
Macroteleia sp.	1	ROMANIA: Iasi, 13.viii.2000, leg. M. Mitroiu
Macroteleia sp.	1	ROMANIA: Iasi, 25.vii.2005, leg. L. Fusu
Orthogonalys pulchella	4	USA, WV, Hardy Co. 3mi NE Mathias, 38°55'N, 78°49'W, 2–15.vii.2004, Malaise trap. D. Smith
Paramesius sp.	1	ROMANIA: Iasi, 10.ix.2005, leg. O. Popovici
Pelecinus polyturator	1	USA: VA: Fairfax Co., Great Falls, 27.vii–4.viii. 2006, leg. D. Smith
Pelecinus polyturator	1	USA: VA: Fairfax Co., Turkey Run, 5–24.viii.2006, leg. D. Smith
Proctotrupes sp.	1	GREECE: Kerkini Nat. Res., 15–17.vii.2007, leg. G. Ramel
Proctotrupes sp.	1	ROMANIA: Iasi, 7.x.2004, leg. O. Popovici
Proctotrupes sp.	1	ROMANIA: Vorona, 21.v.2007, leg. C. Lisenchi
Psilanteris sp.	1	ROMANIA: Bacau, 17.vii.2004, leg. O. Popovici
Ropronia sp	2	USA: Virginia, Fairfax Co., 18–30.v.2007, leg. D. Smith
Scelio sp.	3	ROMANIA: Iasi, 24.viii.2004, leg. O. Popovici
Sparasion sp.1	2	ROMANIA: Iasi county, Bârnova forest, meadow in glade; 12.vii.2007 N46°59.617'; E27°35.452', Leg. Popovici O. & Popovici Mariana YPT
Sparasion sp.2	1	ROMANIA: Iasi county, Bârnova forest, meadow in glade; 12.vii.2007 N46°59.617'; E27°35.452', Leg. Popovici O. & Popovici Mariana YPT
Sparasion sp.2	2	ROMANIA: Iasi county, Botanical Garden; N47°11.167'; E27°32.983'; 26.vii.2007; Leg. Popovici O. YPT
Sparasion sp.3	3	ROMANIA: Constanta county; sand dune natural reservation from Agigea; 27–29.vii.2008; N44°5.184'; E28°38.517'; Leg. Popovici O. & Popovici Mariana YPT
Sparasion sp.4	10	ROMANIA: Constanta county; sand dune natural reservation from Agigea; 27–29.vii.2008; N44°5.184'; E28°38.517'; Leg. Popovici O. & Popovici Mariana YPT
Sparasion sp.5	1	ROMANIA: Tulcea county; forest border, 9 km S of Babadag; 6–7.vii.2009; N44°48.817'; E28°42.41'; Leg. Popovici O. & Fusu L. YPT
Sparasion sp.6	1	ROMANIA: Tulcea county; forest border, 9 km S of Babadag; 6–7.vii.2009; N44°48.817'; E28°42.41'; Leg. Popovici O. & Fusu L. YPT

Taxon	Number of specimens	Data labels
Sparasion sp.7	1	ROMANIA: Tulcea county; forest border, 9 km S of Babadag; 6–7.vii.2009; N44°48.817'; E28°42.41'; Leg. Popovici O. & Fusu L. YPT
Sparasion sp.7	2	GREECE: Kerkini Lake, N.P. Lithotopos, 1–7.viii.2006 leg. G. Ramel
Sparasion sp.8	2	JAPAN: Kitahira, Otsu-shi Shiga-ken, 19–22.vii.2008, leg. T. Yoshida.
Sparasion sp.9	1	UGANDA: Kibale, N.P. Kanyawara Biol. Station, 14–21.xi.2010, leg. S. Katusabe & Co.
Sparasion sp.	1	USA: NC, Raleigh 03.VII.2009 Winkler, Benoit
Sparasion sp.	7	USA: West Virginia, Hardy Co. VIII-11–28–06, D. Smith
Triteleia sp.	1	ROMANIA: Iasi, 8.ix.2004, leg. O. Popovici
Vanhornia sp.	3	USA: VA: Loudoun Co., 1.vi–17.vii.2000, leg. D. Smith

Appendix 2

Anatomical terms used, cross-referenced to an ontological (formal) definition (Hymenoptera Anatomy Ontology; URI = Uniform Resource Identifier).

Abbreviation	Term	Ontological definiton	URI
	acanthae	The process that corresponds to a single epidermal cell.	http://purl.obolibrary.org/obo/HAO_0002119
anh	annular hair	The spine on the distal part of ligula that is connected proximolaterally to the neighboring glossal hair by a carina.	http://purl.obolibrary.org/obo/HAO_0002205
ags	anterior glossal sclerite	The sclerite of the anterior glossal plate that is lateral to the median conjunctiva of the anterior glossal plate.	http://purl.obolibrary.org/obo/HAO_0000112
asg	anterior surface of the glossa	The area of the glossa that is between the distal glossal edge and the anterior glossal plate.	http://purl.obolibrary.org/obo/HAO_0002208
tnta-pmn	anterior tentorio-premental muscle	The muscle that arises anteriorly from the cranium and inserts on the posterior margin of the prementum.	http://purl.obolibrary.org/obo/HAO_0001064
stia-mp1	anterior stipito-palpal muscle	The stipito-palpal muscle that arises medially on the proximal part of the stipes and inserts anteroproximally on the first maxillary sclerite.	http://purl.obolibrary.org/obo/HAO_0000909
conj	anterolateral wall of the stipes	The area that extends between anterior margin of the median wall of the stipes and the lateral margin of the posterior wall of the stipes and the base of the mandible and the labrum.	http://purl.obolibrary.org/obo/HAO_0002215
agh	apical glossal hair	The spines that are on the distal glossal edge.	http://purl.obolibrary.org/obo/HAO_0002209
sts	apical glossal setae	The row of setae of the glossa that is adjacent to the distal glossal edge.	http://purl.obolibrary.org/obo/HAO_0002210
	apicomedial galeal plate	The sclerite that is located on the medial surface of the galeo-lacinial complex and bears the coeloconic sensillum of galea.	http://purl.obolibrary.org/obo/HAO_0002142
bcr	basal cardinal ridge	The cardinal ridge that is median.	http://purl.obolibrary.org/obo/HAO_0002083
bgs	basal galeal sclerite	The sclerite that receives the site of insertion of the stipito-galeal muscle.	http://purl.obolibrary.org/obo/HAO_0002143
inv	basal glossal invagination	The anterior invagination of the labium that is adjacent with the distal end of the salivarium and separates the glossa proximally from the distal hypopharynx and the paraglossae.	http://purl.obolibrary.org/obo/HAO_0002231

bgb	basiparaglossal brush	The anteroproximal area of the paraglossa that is covered with long acanthae and corresponds to the ligament connecting the acroglossal button with the basiparaglossal sclerite.	http://purl.obolibrary.org/obo/HAO_0002199
pls	basiparaglossal sclerite	The sclerite that is located medially on the paraglossa and articulates with the anterior glossal plate and is continuous with the hypopharyngeal rod..	http://purl.obolibrary.org/obo/HAO_0002201
cps	campaniform sensillum	The aporous sensillum without a hairlike cuticular component.	http://purl.obolibrary.org/obo/HAO_0001973
cfs	coeloconic sensillum of galea	The coeloconic sensillum that is located on the medial surface of the galeo-lacinial complex distal to the base of the lacinial lobe.	http://purl.obolibrary.org/obo/HAO_0002141
csg	campaniform sensillum of glossa	The campaniform sensillum of the anterior surface of the glossa that is located proximal to the glossal annuli.	http://purl.obolibrary.org/obo/HAO_0002212
cps	campaniform sensillum of the prementum	The campaniform sensillum that is on the ventral premental face.	http://purl.obolibrary.org/obo/HAO_0002244
	cardinal articular condyle of the cranium	The condyle that is located on the cranium and articulates with the cranial fossa of the cardo.	http://purl.obolibrary.org/obo/HAO_0002074
	cardinal lever	The process that receives the site of attachment of the cranio-cardinal muscle.	http://purl.obolibrary.org/obo/HAO_0002075
cd	cardo	The sclerite that is articulated with the cranium at the cranio-cardinal articulation, is connected to the stipes distolaterally via the stipitocardinal hinge and receives the site of attachment of the cranio-cardinal muscle.	http://purl.obolibrary.org/obo/HAO_0000187
	conjunctiva	The area of the integument that is weakly sclerotized, with thin exocuticle.	http://purl.obolibrary.org/obo/HAO_0000221
caf	cranial fossa of the cardo	The fossa that is located on the cardo and articulates with the cardinal condyle of the cranium.	http://purl.obolibrary.org/obo/HAO_0002219
cr-cd	cranio-cardinal muscle	The maxillar muscle that arises medially from the occiput dorsally of the occipital foramen and inserts on the proximolateral part of the cardo.	http://purl.obolibrary.org/obo/HAO_0001592
	cranio-lacinial muscle	The maxillar muscle that arises from the occiput and inserts on the proximal part of the lacinial lobe.	http://purl.obolibrary.org/obo/HAO_0001593
dge	distal glossal edge	The transverse edge that extends distally on the glossa.	http://purl.obolibrary.org/obo/HAO_0002206
dhi	distal hypopharyngeal invagination	The invagination on the distal hypopharynx that id adjacent to the concavities of the hypopharyngeal rods.	http://purl.obolibrary.org/obo/HAO_0002213
dhy	distal hypopharynx	The area that is located on the anterior surface of the hypopharyngeal wall and is delimited proximally by the infrabuccal pouch or the distal margin of the sitophore, distally by the salivarial orifice and laterally by the lateral parts of the prementum and the hypopharyngeal rods.	http://purl.obolibrary.org/obo/HAO_0001575
dhs	distal hypopharyngeal sclerite	The sclerite that receives the site of insertions of the dorsal and ventral premento-salivarial muscles and is continuous with the hypopharyngeal rod.	http://purl.obolibrary.org/obo/HAO_0002228

dgs	distolateral galeal sclerite	The sclerite that is located distolaterally on the lateral wall of the galeo-lacinial complex and bears the apicolateral galeal setae.	http://purl.obolibrary.org/obo/HAO_0002127
dgp	distolateral galeal setiferous patch	The setiferous patch that is located distolaterally on the galeo-lacinial complex	http://purl.obolibrary.org/obo/HAO_0002128
dmf	distomedial stipital flange	The medial part of the principal carina of the stipes that is overlapped by the premental carina and overlaps the lateral premental face.	http://purl.obolibrary.org/obo/HAO_0002217
pmd-slv	dorsal premento-salivarial muscle	The salivarial muscle that inserts proximodorsally on the salivary duct.	http://purl.obolibrary.org/obo/HAO_0000274
5mp	fifth sclerite of the maxillary palp	The sclerite that is ringlike and is connected distally to the fourth sclerite of the maxillary palp via conjunctiva.	http://purl.obolibrary.org/obo/HAO_0002220
mp1-mp2	first intrinsic muscle of the maxillary palp	The muscle that arises from the first sclerite of the maxillary palp and inserts on the second sclerite of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002114
	first intrinsic muscle of the labial palp	The muscle that arises from the first sclerite of the labial palp and inserts on the second sclerite of the labial palp.	http://purl.obolibrary.org/obo/HAO_0002237
1lp	first sclerite of the labial palp	The sclerite that is ringlike and is connected distolaterally to the prementum via conjunctiva and muscle.	http://purl.obolibrary.org/obo/HAO_0002194
1mp	first sclerite of the maxillary palp	The sclerite that is ringlike and is connected distolaterally to the posterior stipital sclerite via conjunctiva and muscle.	http://purl.obolibrary.org/obo/HAO_0002109
	fourth intrinsic muscle of the maxillary palp	The muscle that arises from the third sclerite of the maxillary palp and inserts on the fourth sclerite of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002222
4mp	fourth sclerite of the maxillary palp	The sclerite that is ringlike and is connected distally to the third sclerite of the maxillary palp via conjunctiva.	http://purl.obolibrary.org/obo/HAO_0002113
	galeal comb	The row of setae that is located on the medial wall of the galeo-lacinial complex proximal to the coeloconic sensilla of galea.	http://purl.obolibrary.org/obo/HAO_0002243
	galeal fringe	The row of setae that extends along the margin of the galeo-lacinial complex, distal to the lacinial lobe.	http://purl.obolibrary.org/obo/HAO_0002133
	galeal lamina	The lobe that is located medially on the internal wall of the galeo-lacinial complex and margined by the galeal comb.	http://purl.obolibrary.org/obo/HAO_0002136
glb	galeal lobe	The lobe that is located on the stipes at the distal part of the posterior stipital sclerite distolateral to the lacinia.	http://purl.obolibrary.org/obo/HAO_0000368
gal-lac	galeo-lacinial complex	The area of the stipes that is delimited proximomedially by the stipito-premental conjunctiva, proximolaterally by the stipito-mandibular conjunctiva and posteroproximally by the margin of the posterior stipital sclerite.	http://purl.obolibrary.org/obo/HAO_0002126
glo	glossa	The lobe of the labium that is limited posteroproximally by the prementum, anteroproximally by the fold traversing the salivary orifice and laterally by the paraglossae.	http://purl.obolibrary.org/obo/HAO_0000376
gla	glossal annuli	The anatomical cluster of the glossa that is composed of annular hairs.	http://purl.obolibrary.org/obo/HAO_0002204
hyb	hypopharyngeal button	The bent area of the hypopharyngeal rod that receives the site of insertion of the posterior tentorio-premental muscle.	http://purl.obolibrary.org/obo/HAO_0002234

hpc	hypopharyngeal pecten	The anterolateral area of the distal hypopharynx that is adjacent with the proximal part of the hypopharyngeal rod proximal to the hypopharyngeal button and is covered with acanthae.	http://purl.obolibrary.org/obo/HAO_0002214
hypr	hypopharyngeal rod	The ligament that connects the proximolateral margin of the prementum with the proximal part of the ligula.	http://purl.obolibrary.org/obo/HAO_0000408
hys	hypostoma	The area that extends on the posterior (ventral) margin of the oral foramen along the site of attachments of the conjunctiva connecting the cranium with the maxillae and is delimited laterally by the pleurostomal fossa.	http://purl.obolibrary.org/obo/HAO_0000411
	integument	The anatomical system that forms the covering layer of the animal, ectodermal in origin and composed of epidermal cells producing the cuticle.	http://purl.obolibrary.org/obo/HAO_0000421
	intercardinal area	The area that is located between the cardines and limited proximally and distally by the anatomical line that extends between the proximal and distal ends of the left and right cardines.	http://purl.obolibrary.org/obo/HAO_0002145
	interstipital area	The area of the postmental area that is limited laterally by the median margins of the stipites, proximally by the anterior margin of the intercardinal area and distally by the proximal margin of the prementum.	http://purl.obolibrary.org/obo/HAO_0002146
	interstipital sclerite	The sclerite that is located on the interstipital area and is connected to the prementum via conjunctiva.	http://purl.obolibrary.org/obo/HAO_0002223
	invagination	The area where the cuticle is invaginated.	http://purl.obolibrary.org/obo/HAO_0002021
	labial palp	The anatomical structure that is distal to the proximal margin of the first sclerite of the labial palp.	http://purl.obolibrary.org/obo/HAO_0000450
pin	labial palpal excision	The notch that is located distolaterally on the prementum and receives the base of the labial palp.	http://purl.obolibrary.org/obo/HAO_0002153
	labium	The appendage that is encircled by the area that is proximally delimited by the lateral margins of the cardo and the posterior stipital sclerite laterally, and the anatomical line that is tangential to the salivary duct and traverses the salivary orifice anteriorly.	http://purl.obolibrary.org/obo/HAO_0000453
	lacinial bar	The sclerite that is located on the lateral wall of the lacinial lobe.	http://purl.obolibrary.org/obo/HAO_0002117
	lacinial comb	The row of setae on the lacinial lobe that is marginal.	http://purl.obolibrary.org/obo/HAO_0002124
bls	lacinial lever	The sclerite that is located on the medial stipital wall and receives the site of insertion of the stipito-lacinial muscle.	http://purl.obolibrary.org/obo/HAO_0002093
llb	lacinial lobe	The lobe that extends proximally on the distal margin of the medial stipital wall, is adjacent to the basal lacinial sclerite, overlaps the proximal part of the galea.	http://purl.obolibrary.org/obo/HAO_0000457
pma	lateral premental face	The area of the prementum, that lays parallel and connected via conjunctiva to the medial stipital vall.	http://purl.obolibrary.org/obo/HAO_0002152

lcr	laterodistal cardinal ridge	The cardinal ridge that arises distally from the basal cardinal ridge and is oriented distolaterally.	http://purl.obolibrary.org/obo/HAO_0002084
	ligament	The area of the cuticle that is resilin rich.	http://purl.obolibrary.org/obo/HAO_0002229
	ligula	The anatomical cluster that is composed of the glossa and paraglossae.	http://purl.obolibrary.org/obo/HAO_0000496
	lobes	The evagination that is mostly membranous.	http://purl.obolibrary.org/obo/HAO_0001587
md	mandible	The sclerite that is connected to the cranium along the anterior margin of the oral foramen via the anterior and posterior cranio-mandibular articulations.	http://purl.obolibrary.org/obo/HAO_0000506
mfs	marginal fringe of the stipes	The anatomical cluster that is composed of the spines on the distal margin of the distolateral portion of the principal carina of the stipes.	http://purl.obolibrary.org/obo/HAO_0002216
	maxilla, maxillae	The appendage that is encircled by the area that is proximally delimited by the hypostoma posteriorly, the median margin of the mandible laterally, the labrum anterolaterally and the labium medially.	http://purl.obolibrary.org/obo/HAO_0000513
mpalp	maxillary palp	The anatomical structure that is distal to the proximal margin of the first sclerite of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0000515
	maxillary palpal sclerite	The sclerite that is part of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002183
	maxillary process of the hypostoma	The articular process that bears the cardinal condyle of the cranium.	http://purl.obolibrary.org/obo/HAO_0002073
	maxillo-labial complex	The anatomical cluster that is composed of the maxillae and the labium and is connected by conjunctivae laterally to the cranium along the hypostoma, to the mandible along the proximomedial margin of the mandible and proximally to the hypopharynx.	http://purl.obolibrary.org/obo/HAO_0000452
msh	mechanosensory hair	The aporous sensillum that has a hair-like cuticular component.	http://purl.obolibrary.org/obo/HAO_0001039
msg	medial stipital groove	The depression that extends medially and adjacent to the medial portion of the principal carina of stipes.	http://purl.obolibrary.org/obo/HAO_0002106
	medial wall	The area that is medial and lays parallel with the lateral wall of the prementum.	http://purl.obolibrary.org/obo/HAO_0002092
	median conjunctiva of the anterior glossal plate	The median conjunctiva of the anterior glossal plate that is parallel with the anteroposterior body axis.	http://purl.obolibrary.org/obo/HAO_0002203
mpr	median postmental ridge	The ridge that is limited laterally by the stipital articular surfaces of the postmentum.	http://purl.obolibrary.org/obo/HAO_0002225
mcr	mediodistal cardinal ridge	The cardinal ridge that arises distally from the basal cardinal ridge and is oriented distomedially.	http://purl.obolibrary.org/obo/HAO_0002085
pgl	paraglossa	The lobe that is connected to the distal margin of the prementum posteroproximally, to the premental hypopharynx proximolaterally and anteroproximally, to the glossa proximomedially and bears the basiparaglossal brush and the paraglossal sclerite.	http://purl.obolibrary.org/obo/HAO_0000686

pgb	paraglossal acroglossal button	The sclerite that is located distally on the paraglossa.	http://purl.obolibrary.org/obo/HAO_0002232
	paraglossal annuli	The anatomical cluster of the paraglossa that is composed of connected annular hairs.	http://purl.obolibrary.org/obo/HAO_0002233
	paraglossal sclerite	The anteroproximal sclerite of the paraglossa that bears the basiparaglossal brush.	http://purl.obolibrary.org/obo/HAO_0002200
pgp	posterior glossal plate	The sclerite that is connected to the distal margin of the prementum and receives the site of insertion of the premento-paraglossal muscles.	http://purl.obolibrary.org/obo/HAO_0000747
pss	posterior stipital sclerite	The sclerite that is located on the posterior stipital wall, articulates with the cardo and with the labial palp, is connected by conjunctiva distolaterally to the galeo-lacinial complex, proximally to the hypostoma and the cardo, proximolaterally to the mandible.	http://purl.obolibrary.org/obo/HAO_0002097
stip-mp1	posterior stipito-palpal muscle	The stipito-palpal muscle that arises medially on the proximal part of the stipes and inserts posteroproximally on the first maxillary palpal segment.	http://purl.obolibrary.org/obo/HAO_0001814
	posterior wall	The area that is limited medially by the medial stipital wall and limited proximolaterally by the margin of the posterior stipital sclerite.	http://purl.obolibrary.org/obo/HAO_0002097
pwg	posterior surface of the glossa	The area of the glossa that is between the distal margin of the prementum and the distal glossal edge.	http://purl.obolibrary.org/obo/HAO_0002207
tntp-pmn	posterior tentorio-premental muscle	The tentorio-labial muscle that arises from the cranium and inserts distally on the labium adjacent to the level of the salivary orifice.	http://purl.obolibrary.org/obo/HAO_0000264
	postmental area	The area that is limited distally by the posterior margin of the prementum and laterally by the median margins of the cardines and the stipites.	http://purl.obolibrary.org/obo/HAO_0002144
pph	postmental-premental hinge	The conjunctiva that is between the postmentum and prementum.	http://purl.obolibrary.org/obo/HAO_0002226
	postmento-premental muscle	The labial muscle that is unpaired, arises from the postmentum and inserts on the proximal margin of the prementum.	http://purl.obolibrary.org/obo/HAO_0000803
psm	postmentum	The anatomical cluster that is composed of the sclerites that are on the postmental area.	http://purl.obolibrary.org/obo/HAO_0000785
prm	premental arms	The area of the lateral premental face that receives the site of origin of the dorsal premento-salivarial muscle.	http://purl.obolibrary.org/obo/HAO_0002155
pmc	premental carina	The flange that is adjacent with the border between the ventral and lateral premental faces and that overlaps externally the median part of the posterior stipital sclerite.	http://purl.obolibrary.org/obo/HAO_0002157
pmd	premental ditch	The scrobe of the prementum that is adjacent to and extends lateral to the premental carina and accommodates the medial part of the posterior stipital sclerite.	http://purl.obolibrary.org/obo/HAO_0002227
	premento-glossal muscle	The labial muscle that arises on the ventral part of the prementum, laterally to the ventral premento-salivarial muscle and inserts on the anterior glossal plate.	http://purl.obolibrary.org/obo/HAO_0000377

	premento-palpal muscle	The labial muscle that arises from the prementum and inserts on the first sclerite of the labial palp.	http://purl.obolibrary.org/obo/HAO_0000314
pmn-pgs	premento-paraglossal muscle	The labial muscle that arises from the ventral part of the prementum, anterior to the origin of the premento-glossal muscle and ventral premento-salivarial muscle and inserts just distally of the distal margin of the prementum.	http://purl.obolibrary.org/obo/HAO_0000687
pmn	prementum	The sclerite that is median, is connected via conjunctiva along its proximolateral margins to the stipites, is articulated with the labial palps, is continuous along its distal margin with the ligula and distolateral margins with the distal hypopharynx and receives the site of attachments of the extrinsic labial palp muscles.	http://purl.obolibrary.org/obo/HAO_0000804
pcs	principal carina of the stipes	The flange that extends along the margin of the posterior stipital wall.	http://purl.obolibrary.org/obo/HAO_0002099
	proximal galeal brush	The row of setae that is on the distal margin of the proximolateral galeal sclerite.	http://purl.obolibrary.org/obo/HAO_0002135
pgs	proximolateral galeal sclerite	The sclerite that is located on the lateral wall of the galeo-lacinial complex and bears the proximolateral galeal setiferous patch.	http://purl.obolibrary.org/obo/HAO_0002130
prs	proximolateral galeal setiferous patch	The setiferous patch that is located on the lateral wall of the galeo-lacinial complex proximally of the distolateral setiferous patch.	http://purl.obolibrary.org/obo/HAO_0002129
pmf	proximomedial stipital flange	The medial part of the principal carina of the stipes that is overlapped distally by the distomedial stipital carina and overlaps the lateral premental face and the proximal part of the prementum.	http://purl.obolibrary.org/obo/HAO_0002218
svr	salivarium	The area that is at the proximal end of the salivary duct and corresponds to the site of insertion of the dorsal and ventral premento-salivarial muscles.	http://purl.obolibrary.org/obo/HAO_0000906
svd	salivary duct	The duct that leads from the salivary gland.	http://purl.obolibrary.org/obo/HAO_0002236
	salivarial sclerite	The sclerite that is located in the ventral wall of the salivarium and corresponds to the site of insertion of the ventral premento-salivarial muscle.	http://purl.obolibrary.org/obo/HAO_0001682
	sclerite	The area of the integument that is strongly sclerotised, with thick exocuticle and is surrounded by conjunctivae.	http://purl.obolibrary.org/obo/HAO_0000909
	second intrinsic muscle of the maxillary palp	The muscle that arises from the first sclerite of the maxillary palp and inserts on the third sclerite of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002115
	second intrinsic muscle of the labial palp	The muscle that arises from the second sclerite of the labial palp and inserts on the third sclerite of the labial palp.	http://purl.obolibrary.org/obo/HAO_0002238
	second sclerite of the labial palp	The sclerite that is ringlike and is connected distally to the first sclerite of the labial palp via conjunctiva and muscle.	http://purl.obolibrary.org/obo/HAO_0002195
	second sclerite of the maxillary palp	The sclerite that is ringlike and is connected distolaterally to the first sclerite of the maxillary palp via conjunctiva and muscle.	http://purl.obolibrary.org/obo/HAO_0002111

	seta	The sensillum that is multicellular and consists of trichogen, tormogen, and sense cells and the cuticle secreted by and adjacent to the trichogen cell.	http://purl.obolibrary.org/obo/HAO_0000935
	skeletal muscle	The muscle that is attached at either end to the cuticle.	http://purl.obolibrary.org/obo/HAO_0001922
	spiculate patch of galea	The area on the galeo-lacinial complex distal to the lacinial lobe that is covered with acanthae.	http://purl.obolibrary.org/obo/HAO_0002139
	spiculate patch of the lacinia	The area on the lacinial lobe that is covered with acanthae.	http://purl.obolibrary.org/obo/HAO_0002138
	spine	The process that lacks non-sclerotised ring at the base.	http://purl.obolibrary.org/obo/HAO_0000949
	stipes, stipites	The appendage that is connected posteroproximally to the hypostoma, anteroproximally and lateroproximally to the mandible and medioproximally to the labium and the hypopharynx via conjunctiva, is connected to the cranium via muscles and that bears the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0000958
	stipital sclerite	The sclerite that is on the medial stipital wall, bears the medial stipital process.	http://purl.obolibrary.org/obo/HAO_0002096
sti-gal	stipito-galeal muscle	The maxillar muscle that arises from the posterior sclerite of the stipes medial to the site of origin of the stipito-lacinial muscle and inserts on the median wall of the galeo-lacinial complex distal to the stipito-lacinial muscle.	http://purl.obolibrary.org/obo/HAO_0001661
sti-lac	stipito-lacinial muscle	The maxillar muscle that arises along the lateral margin of the posterior stipital sclerite and inserts proximally on the median wall of the stipes just proximal to the lacinal lobe.	http://purl.obolibrary.org/obo/HAO_0001660
sti-mp1	stipito-palpal muscle	The maxillary muscle that arises from the posterior stipital sclerite and inserts on the first sclerite of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002110
	stipito-premental conjunctiva	The conjunctiva that extends along the posterior (dorsal) margin of the premental arm and the proximal margin of the medial stipital wall.	http://purl.obolibrary.org/obo/HAO_0002125
sch	stipitocardinal hinge	The membranous area linking the cardo and stipes.	http://purl.obolibrary.org/obo/HAO_0002076
sts	styloconic sensillum	The seta that is on a process.	http://purl.obolibrary.org/obo/HAO_0002211
tnt-cd	tentorio-cardinal muscle	The maxillary muscle that arises from the anterior region of the cranium and inserts adjacent to the cardino-stipital hinge.	http://purl.obolibrary.org/obo/HAO_0001638
tnt-sti	tentorio-stipital muscle	The maxillar muscle that arises on the posteroventral part of the anterior tentorial arm and inserts on the median wall of the stipes.	http://purl.obolibrary.org/obo/HAO_0001002
	tentorium	The apodeme that has its sites of origin marked by the anterior and posterior tentorial pits and gular sulci.	http://purl.obolibrary.org/obo/HAO_0001003
	third intrinsic muscle of the maxillary palp	The muscle that arises from the second sclerite of the maxillary palp and inserts on the third sclerite of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002116
	third sclerite of the labial palp	The sclerite that is ringlike and is connected distally to the second sclerite of the labial palp via conjunctiva and muscle.	http://purl.obolibrary.org/obo/HAO_0002196

3mp	third sclerite of the maxillary palp	The sclerite that is ringlike and is connected distally to the second segment of the maxillary palp via conjunctiva and muscle.	http://purl.obolibrary.org/obo/HAO_0002112
ss1	uniporous sensilla, Type 1 seta	The sensillum whose cuticular component has one cuticular pore.	http://purl.obolibrary.org/obo/HAO_0002221
vlm	velum	The flange that is transparent, and extends along the anterodistal margin of the galeo-lacinial complex distal to the lacinial lobe.	http://purl.obolibrary.org/obo/HAO_0002140
vdp	ventral dististipital process	The projection that is located distally on the posterior stipital sclerite and encircles the base of the maxillary palp.	http://purl.obolibrary.org/obo/HAO_0002102
	ventral glossal lines	The carinae that radiates from the posterior glossal plate towards the apical glossal setae.	http://purl.obolibrary.org/obo/HAO_0002230
vpf	ventral premental face	The area of the prementum that is delimited laterally by the lateral premental face.	http://purl.obolibrary.org/obo/HAO_0002156
pmnv-slv	ventral premento-salivary sclerite muscle	The salivarial muscle that arises from the proximal end of the ventral part of the prementum and inserts on the salivarial sclerite.	http://purl.obolibrary.org/obo/HAO_0001072
vba	ventrolateral basiglossal arm	The projection that is located proximolaterally on the anterior glossal plate and articulates with the basiparaglossal sclerite.	http://purl.obolibrary.org/obo/HAO_0002202

Appendix 3

Volume rendered CLSM media files on figshare.com

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